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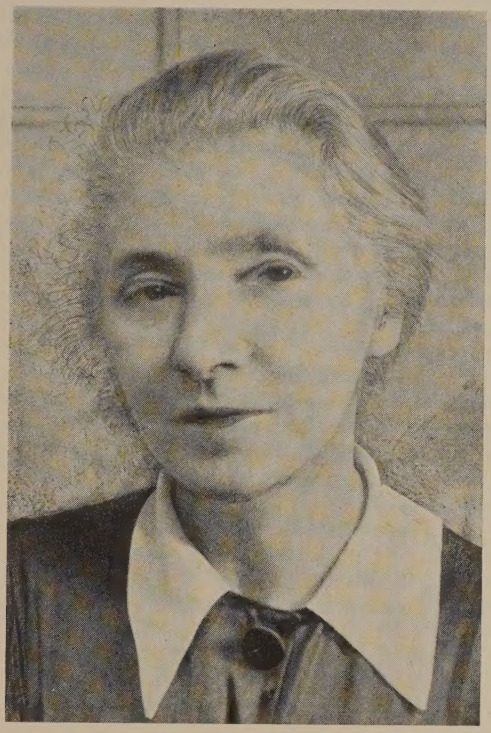

Helen Ogilvie
1880—1960

It is with regret that we announce the death of Miss Helen S. OGILVIE in her 80th year. She was born in Dundee, Scotland, on 17th May 1880, and later studied under Sir D'Arcy W. THOMPSON at St. Andrew's University, where she obtained the degrees of M.A., B.Sc., with special distinction in Botany and Zoology. She then specialized in marine phytoplankton under Prof. H. H. GRAN at Oslo.

Miss OGILVIE was appointed to the staff at the Aberdeen Laboratory

(then under the Fishery Board for Scotland) in 1911 where she worked mainly on the identification of phytoplankton and the planktonic food of fishes until her retirement in 1946. From 1920 to 1926 she was temporarily transferred to Dundee to act as assistant to Prof. D'Arcy THOMPSON who was Scientific Advisor to the Board. Her papers included several in the Council's series including her section in GRAN's paper in the *Bulletins Planktoniques* and two in the *Rapports et Procès-Verbaux*. She continued her interest after she retired and remained voluntarily at the laboratory, during which time she produced the first sheet on copepod nauplii in the *Fiches d'Identification du Zooplancton* (Sheet 50), and did much towards the second sheet (Sheet 63) but had to discontinue because of gradually failing eyesight. Her keen interest in microscopy was inherited from her father, a tea and coffee blender whose hobby was the study and mounting of diatoms.

A keen mountaineer, there was hardly a mountain in Scotland she had not climbed and in days when transport was meagre; she also loved her garden and her music. She was very independent in spirit and had lived alone since 1926, even during the last years of her life when her eyesight was all but useless. She died peacefully on 29th May 1960, at her home in West Newport, by Dundee, and as she would have wished, retaining her other faculties and her independence to the last.

J. H. Fraser

On the Alkalinity of Baltic Waters

By

Stina Gripenberg

Marine Research Institute, Helsinki

Introduction

According to the definition given by HELLAND-HANSEN, JACOBSEN, and THOMPSON (1948) the alkalinity is "the quantity of anions, excepting those of strong acids" contained in 1 litre of sea water at 20°C. As is well known, the most important "non-strong" acids are carbonic acid and boric acid. While in oceanic water the alkalinity is closely proportional to the chlorinity, this is not true of Baltic water. The linear relationship existing between the two quantities here contains a constant term which is due to the influence of the great quantities of river water of varying composition flowing into the Baltic. Some of the affluents, passing through areas of primitive rocks, are practically lime-free while others transport high amounts of carbonates into the sea. It is therefore natural that different equations relating the alkalinity and the chlorinity are valid in different parts of the Baltic. These equations, however, vary from year to year and, in addition, single alkalinity values never fit well into any equations, two facts which indicate that the amount of carbonates in the water also varies, carbonate and bicarbonate ions being the principal anions of "non-strong", i. e. weak acids in the water. If these conclusions are correct the amount of calcium and magnesium ions should also vary, since the excess of carbonate ions are furnished by the solution of calcium and magnesium carbonates. But contrary to expectations, both calcium and magnesium have been found to be regularly distributed. The calcium concentrations in the different basins fit well into linear equations, which do not vary from year to year, while the magnesium concentrations are, on an average, directly proportional to the chlorinities over the whole of the Baltic, the ratio being the same as for oceanic water. This shows that the explanation given above for the variations of the alkalinity is not sufficient. There must exist in Baltic water other anions of weak acids, which have their own rhythm of variation and which seemingly erratically influence the alkalinity values. In the present paper the assumption is put forth that organic acids here reveal their presence. An attempt is made to evaluate in milliequivalents the amounts of these non-accounted-for anions in a number of samples from eight stations in the Gulf of Bothnia and the Baltic proper. The unknown anions, which of course may be of more than

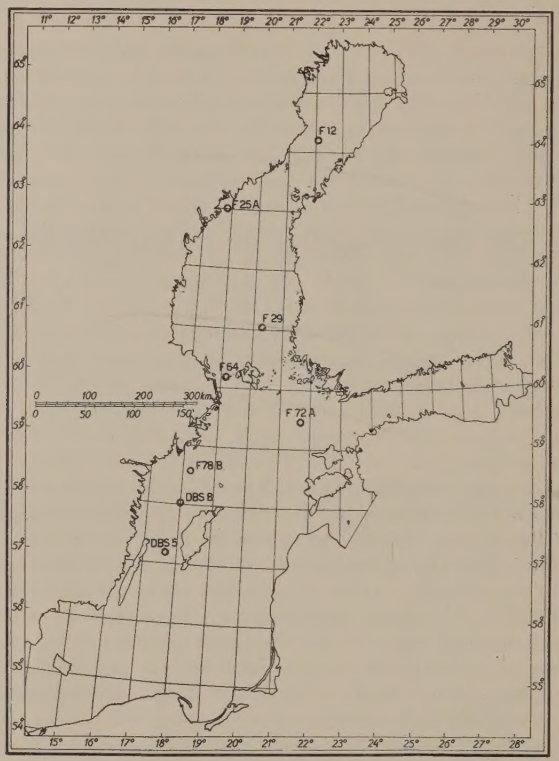

Figure 1. Hydrographical stations.

one kind, are designed by a common name as the "surplus alkalinity". It is suggested that part or the whole of it may be formed of complex anions of organic decomposition products coupled with boric acid. It should be pointed out that the surplus alkalinity is not identical with the total organic matter in Baltic water, but may perhaps serve as a rough measure thereof in that a high surplus alkalinity may indicate a high amount of organic matter.

Samples and Analyses

During the regular summer cruises organized in June 1957 by the Marine Research Institute of Helsinki on board the research ship "Aranda", 65 water samples to be analysed for alkalinity were collected from 8 stations in the Gulf of Bothnia and in the Baltic proper (Figure 1).

The samples were analysed by indirect titration. To 100 ml of water 15 ml of 0·012–n HCl were added. The CO_2 set free was expelled by passing CO_2-free air through the solution for at least half an hour after which the excess acid was titrated with 0·012–n NaOH, methyl red (0·1 g of the Na salt dissolved in

100 ml of ethyl alcohol) being used as indicator. Electrometric titrations using the Beckman pH-meter and in the presence of the indicator, showed that the equivalence point coincided with the appearance of the purely alkaline colour. For accurate results it is convenient to use as a colour standard an alkaline solution with the same indicator concentration as in the analysis (see, however, the discussion on the equivalence point, p. 18). The alkalinity values in milliequivalents per litre were reduced by calculation to milliequivalents per kilogramme of sea water. The accuracy of the titration thus performed may be evaluated at $\pm$ one drop or $\pm$ 0·004 meq/kg. This corresponds to 0·25–0·50 % of the alkalinity.

Thirteen surface and bottom samples were titrated electrometrically and at the same time analysed for boron. When the alkalinity titration was ready 5 g of mannitol were added and the titration continued. The mean equivalence point for the thirteen samples was pH 7·37, the range being 7·15 to 7·67.

Results

The results of the analyses are presented in Table 1. Columns 1, 2, and 3 give the depths in metres, Cl $^0/_{00}$ and the alkalinity in meq per kg respectively,*) columns 6 and 7 the boron concentrations in mg-at per kg or, what amounts to the same, H_3BO_3 meq/kg and the ratio B/Cl. Boron seems to occur in a slightly higher concentration in the Baltic than in the oceans. The mean ratio of B mg-at/kg to Cl $^0/_{00}$ for the 13 analyses is 0·0244, corresponding to B $^0/_{00}$ / Cl $^0/_{00}$ = 0·000264 or H_3BO_3 $^0/_{00}$ / Cl $^0/_{00}$ = 0·00151. LYMAN and FLEMING's "present best value" for the last ratio is 0·00137 (quoted after BARNES (1955)).

The alkalinities are shown graphically in Figures 2 a and b (p. 10). Here the depth coordinate is the same for all stations, but the origins of the chlorinity and the alkalinity value are successively displaced towards the right. It is seen that the alkalinities, as expected, on the whole follow the chlorinities. It is, however, noteworthy that at four stations, F25A, F29, F64, and DBS5 there is a slight decrease of the alkalinity at the bottom though the corresponding chlorinities increase or remain constant. At F64 this decrease is felt already at 25 m from the bottom. The decrease at DBS5 is perhaps only apparent and due to the exceptionally and maybe accidentally high alkalinity at 80 m. A duplicate analysis on a smaller amount of water, however, confirmed the high value. In general, it was not possible to make duplicate analyses owing to the small volume of the samples.

Discussion

The small number of stations does not allow the computation of equations expressing the relationship between the alkalinity and the chlorinity and in view of the fact that Baltic alkalinity values are always more or less scattered and never agree well with calculated linear equations, such a computation would not offer much interest. The general equations calculated by BUCH

*) The chlorinity for F12, 0 m, has been changed. It was 1·73 $^0/_{00}$, a value which agreed neither with the alkalinity, nor with the boron content. At this station the sample for 80 m was titrated electrometrically, not the bottom sample.

Table 1

Analyses of alkalinity and boron in Baltic water

Depth in metres	Chlorinity	Alkalinity	Minimum alkalinity	Surplus alkalinity	B	
1	2	3	4	5	6	7
m	$Cl^0/_{00}$	Alk meq/kg	Alk_{min} meq/kg	Alk_x meq/kg	mg–at/kg H_3BO_3 meq/kg	B/Cl
			F12, 64°03′ N, 22°04′ E			
0	1·96	0·811	0·744	0·067	0·048	0·0245
20	1·96	0·812	0·744	0·068		
40	2·05	0·854	0·774	0·080		
60	2·32	0·937	0·863	0·074		
80	2·42	0·971	0·896	0·075	0·058	0·0240
110	2·55	1·006	0·939	0·067		
			F25A, 62°59·5′ N, 18°51′ E			
0	2·97	1·157	1·078	0·079	0·069	0·0232
20	3·13	1·212	1·131	0·081		
40	3·28	1·266	1·181	0·085		
60	3·49	1·321	1·250	0·071		
80	3·67	1·373	1·310	0·063		
100	3·68	1·372	1·313	0·059		
150	3·74	1·389	1·333	0·056		
175	3·75	1·392	1·336	0·056		
189	3·75	1·381	1·336	0·045	0·096	0·0256
			F29, 61°03′ N, 20°16′ E			
0	3·25	1·242	1·171	0·071	0·084	0·0258
20	3·24	1·239	1·167	0·072		
40	3·32	1·263	1·194	0·069		
60	3·32	1·293	1·194	0·099		
80	3·64	1·361	1·300	0·061		
100	3·76	1·355	1·340	0·015	0·094	0·0250
			F64, 60°11·5′ N, 19°09′ E			
0	3·09	1·211	1·118	0·093	0·074	0·0240
20	3·33	1·277	1·197	0·080		
40	3·69	1·392	1·316	0·076		
60	3·76	1·425	1·340	0·085		
80	3·84	1·448	1·366	0·082		
100	3·86	1·438	1·373	0·065		
150	3·92	1·439	1·393	0·046		
200	3·98	1·461	1·412	0·049		
250	3·99	1·435	1·416	0·019		
275	4·00	1·414	1·419	−0·005	0·094	0·0235
			F72A, 59°27′ N, 21°49′ E			
0	3·50	1·382	1·225	0·157	0·079	0·0226
20	3·85	1·428	1·306	0·122		
40	4·00	1·464	1·341	0·123		
60	4·46	1·507	1·448	0·059		
80	5·69	1·610	1·471	0·139		
100	5·91	1·634	1·485	0·149		
125	5·95	1.642	1.487	0.155	0.151	0.0254

Table 1 (continued)

Depth in metres	Chlorinity	Alkalinity	Minimum alkalinity	Surplus alkalinity	B	
1	2	3	4	5	6	7
m	$Cl^0/_{00}$	Alk meq/kg	Alk_{min} meq/kg	Alk_x meq/kg	mg–at/kg H_3BO_3 meq/kg	B/Cl
			F78B, 58°36′ N, 18°15′ E			
0	3·50	1·308	1·225	0·083	0·084	0·0240
20	3·78	1·387	1·290	0·097		
40	3·96	1·418	1·332	0·086		
60	4·29	1·494	1·408	0·086		
80	5·61	1·630	1·467	0·163		
100	5·81	1·638	1·479	0·159		
150	6·00	1·640	1·490	0·150		
200	6·04	1·634	1·492	0·142		
250	6·04	1·656	1·492	0·164		
300	6·11	1·662	1·497	0·165		
350	6·11	1·650	1·497	0·153		
400	6·14	1·658	1·498	0·160		
425	6·16	1·663	1·500	0·163	0·148	0·0240
			DBS8, 58°00·5′ N, 18°01′ E			
0	3·68	1·396	1·267	0·129	–	–
20	3·85	1·400	1·306	0·094		
40	3·98	1·456	1·336	0·120		
60	4·25	1·457	1·399	0·058		
80	5·53	1·555	1·462	0·093		
100	5·77	1·609	1·476	0·133		
150	5·88	1·619	1·483	0·136		
186	5·88	1·638	1·483	0·155	–	–
			DBS5, 57°09′ N, 17°40′ E			
0	3·94	1·427	1·327	0·100	0·101	0·0256
20	3·95	1·453	1·329	0·124		
40	4·02	1·458	1·346	0·112		
60	4·39	1·530	1·431	0·099		
80	5·51	1·650	1·461	0·189		
105	5·71	1·615	1·473	0·142	–	–

(1945, p. 90) give too high values all through, but neither is in good agreement to be expected as is shown by the equations for the separate years (1932–1936) which vary considerably. It may be argued and probably with a certain justification that the bad agreement might be due to the difference in method, my samples having been treated with CO_2-free air at room temperature for expelling the carbon dioxide liberated by the acid whereas boiling was used for the older material. This circumstance, however, can only account for a fraction of the deviations observed. The principle explanation must be sought elsewhere. It is also worth mentioning that the air current method was used on 75 samples from the Barents Sea and they gave on an average the same relation between the alkalinity and the chlorinity as is accepted for Atlantic water, viz., Alk meq/l $= 0{\cdot}123$ Cl $^0/_{00}$ (WATTENBERG, 1933).

It is well known that the alkalinity is much higher in the Baltic compared with the chlorinity than in oceanic water. This is ascribed to bicarbonates and carbonates brought down by river water, but may also in part be due to anions of organic acids transported by rivers or formed as a result of the metabolism within the sea.

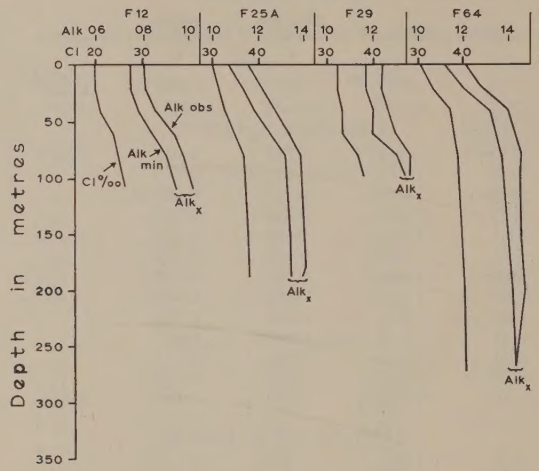

Figure 2a. Variation with depth of the chlorinity and the minimum, observed and surplus alkalinities at the Gulf of Bothnia stations.

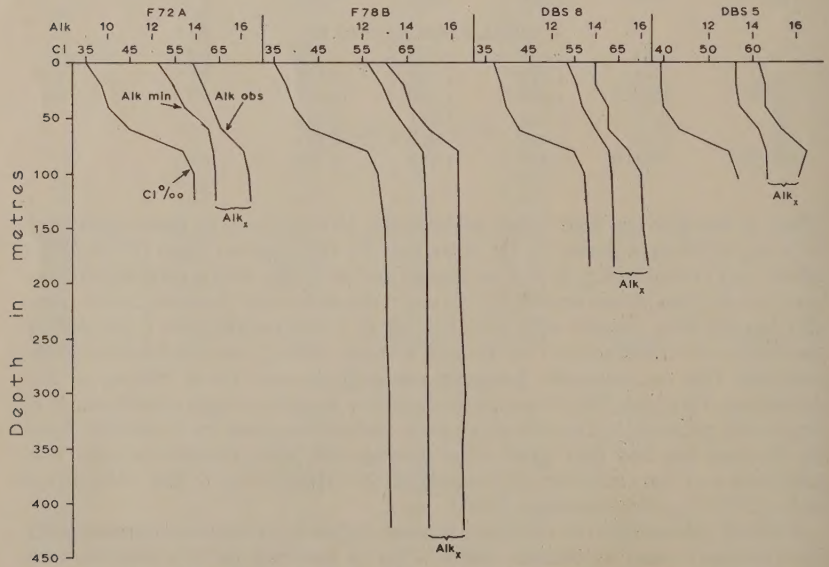

Figure 2b. Variation with depth of the chlorinity and the minimum, observed and surplus alkalinities at the Baltic proper stations.

The organic matter brought to the sea by rivers is far from negligible. On the basis of Swedish, Finnish and to a certain extent, Russian and Estonian analyses of river water the author (GRIPENBERG, 1934) calculated the mean annual addition of organic matter to the Baltic at 12·2 million tons—determined as ignition loss on evaporation residue of filtered water—corresponding to almost 60 g per square metre of sea surface. The greater part thereof is in colloidal solution and nothing is known of the amount that becomes chemically dissolved in the water. The end product of the mineralization, the carbonic acid in its various forms, is accessible to analysis, not so the intermediate stages of the process.

It is generally assumed that the presence of organic compounds does not show up in the alkalinity value. In order to investigate this point the author has tried in the present work a new way of treating the material. This consisted in using well established relationships, not varying from year to year, for calculating approximate alkalinities with the object to account for as great a part as possible of the alkalinities found by analysis. There are three such relationships: (1) that between the alkalinity and the chlorinity in oceanic water, (2) that between the concentration of calcium + strontium ions and the chlorinity in oceanic, and (3) in Baltic water. The idea of considering these relationships in discussing Baltic alkalinities is not new, but BUCH as well as WITTIG (1940) applied them to the general equations only, whereas here I have used the single alkalinity values. This procedure gives the differences between actual and calculated values increased significance.

When the alkalinities are recalculated on a kilogramme basis, the equation relating the alkalinity and the chlorinity in oceanic water becomes:—

$$\text{Alk meq/kg} = 0{\cdot}120\ \text{Cl}\ {}^{0}/_{00} \qquad \ldots\ (1)$$

The equation chosen for calculating the calcium concentration in oceanic water was the one used by WATTENBERG (1933):—

$$\text{Ca mg/kg} = 21{\cdot}56\ \text{Cl}\ {}^{0}/_{00} \text{ or Ca meq/kg} = 1{\cdot}078\ \text{Cl}\ {}^{0}/_{00} \qquad \ldots\ (2)$$

As to the concentration of the calcium ion in Baltic water, there are four equations valid in the separate water masses. The following three, recalculated on a meq/kg basis, are of interest in the present connexion:—

Bottom water, Baltic ..... $\text{Ca meq/kg} = 1{\cdot}130 + 1{\cdot}018\ \text{Cl}\ {}^{0}/_{00}$ .... (3)

Surface water, Baltic and Gulf of Finland ..... $\text{Ca meq/kg} = 0{\cdot}413 + 1{\cdot}191\ \text{Cl}\ {}^{0}/_{00}$ .... (4)

Surface and bottom water, Gulf of Bothnia..... $\text{Ca meq/kg} = 0{\cdot}095 + 1{\cdot}289\ \text{Cl}\ {}^{0}/_{00}$ .... (5)

These equations are founded on 40 analyses made by the author (GRIPENBERG, 1937) according to a method involving a single precipitation of the calcium ion with ammonium oxalate. The standard deviations for the three equations were found to be $\pm$ 0·030, $\pm$ 0·025, and $\pm$ 0·015 meq/kg respectively, the average deviation calculated on the whole material was 0·02 meq/kg or about 0·45%.

The author is not unaware of the criticism which has been raised against her method (ROBERTSON and WEBB, 1939; BARNES, 1955). ROBERTSON and

WEBB found spectrophotometrically that the precipitates were contaminated with sodium and magnesium oxalate and that, on the other hand, part of the calcium remained in solution. The errors were of the order of 2 to 3 %. This does not alter the fact that the greatest deviation of any observed Ca value from the calculated relationships quoted above was 0·6 % and the average deviation less than 0·5 %, a circumstance which is not unimportant when judging the value of the method. It is, as a matter of fact, unessential what metals enter the precipitate, since it is the oxalate therein which is determined and not the calcium. It is the time of digestion which is all important. The accuracy thus depends upon a compensation of errors, a peculiarity which the method shares with many others. The equation for Baltic bottom water was confirmed in an extensive investigation by Hanna WITTIG (1940) who used the method with minor modifications. WITTIG found identical or almost identical equations—hers are given with one decimal place less than the author's—for the bottom water in the basins of the southern Baltic. Somewhat surprisingly the author's equation was also found valid for surface samples collected on a voyage Oslo-Kiel through the Great Belt, thus for chlorinities much higher than those occurring in the northern and central Baltic on which it was founded. This result, which reflects the manner of formation of Baltic bottom water, speaks against large systematical errors in the analyses. More important for judging the value of the method are 150 calcium and magnesium analyses recently published by KOROLEFF and FINNILÄ (1955) and by VOIPIO (1957) and founded on a completely different method. These workers for the first time used complexometric titration with Complexone III or EDTA, the di-sodium salt of ethylenediaminetetraacetic acid, in an extensive study of sea water. VOIPIO was chiefly interested in the magnesium concentration which he presented in the form of the ratio Mg/Cl. The magnesium content is found as the difference between two titrations:— in the first Mg + Ca + Sr is determined, in the second Ca + Sr. VOIPIO having kindly put his analyses at the author's disposal, it was possible to draw up the diagram (Figure 3) where all VOIPIO's and FINNILÄ's Ca + Sr analyses for the Gulf of Bothnia and the Baltic have been introduced and, in addition, the lines corresponding to the author's equations (3), (4), and (5). As to the accuracy of the complexometric Ca determination, VOIPIO (1959) states that negative errors up to 1·5 % are possible. The figure shows in fact that the lines form the upper limit of the complexometric values of which about 40 % lie on the lines or do not differ by more than 0·02 mg-at from these. VOIPIO's analyses include a few of water of high chlorinity from the Kattegat (Table 2). These show a very good agreement between the two methods.

Table 2

Comparison between complexometric Ca analyses and values calculated from the author's equation for Baltic bottom water

	Ca mg–at/kg		
Cl	VOIPIO	GRIPENBERG	Difference
12·92	7·10	7·14	0·04
18·57	10·01	10·02	0·01
18·80	10·08	10·13	0·05
19·19	10·29	10·33	0·04

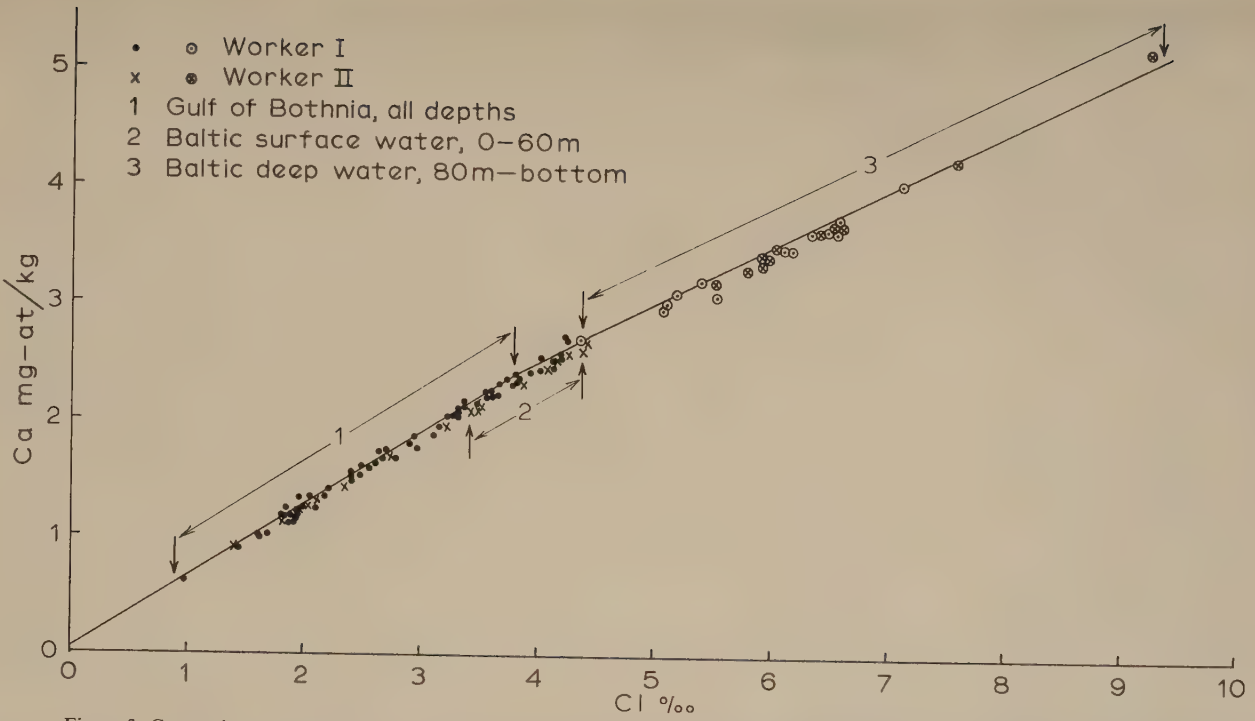

Figure 3. Comparison of the calcium analyses made by FINNILÄ and VOIPIO with those of the author. The latter are given as straight lines corresponding to linear equations valid for the Gulf of Bothnia, Baltic surface water, and Baltic deep water. Arrows indicate extreme chlorinities of the water samples concerned.

The systematical differences here may be said to lie within the permissible analytical errors. This proves again that the author's equation (3) for Baltic bottom water is valid for much higher chlorinities than those for which it was calculated and still more for these. Since the standard deviations for equations (4) and (5) were smaller than for (3), the two first are probably also accurate and all three equations can safely be used for calculating approximate alkalinities in the different water masses of the Baltic.

As to the possible influence of dissolved magnesium carbonate on the alkalinity value, nothing could be said until the recent publications by VOIPIO and by FINNILÄ. According to VOIPIO the ratio of Mg to Cl is constant within a few per cent over the whole of the Baltic, the average being

$$\text{Mg mg-at/kg/Cl } {}^0/_{00} = 0{\cdot}275,$$

a value which lies within the narrow range of ratios valid for different parts of the oceans. There is thus no excess of magnesium in the Baltic or, in other words, in river water dissolved magnesium carbonate as a deliverer of bicarbonate ions to the Baltic, may be left out of consideration. This is, of course, not strictly true since we know that rivers do bring down Mg- and Cl-ions and the Mg-ions may derive from dissolved carbonate. But since in this case the ratio Mg/Cl in the river water, on an average, must be equal to that in the sea, the Mg-ions may have another origin. The constant ratio is perhaps a consequence of the fact that wide land areas bordering on the Baltic were covered by the sea at one time or another after the last ice age. In any case, it is safe to assume that the increased alkalinity in the Baltic is chiefly due to dissolved calcium carbonate. This has always been taken for granted and has now been confirmed by VOIPIO's and FINNILÄ's magnesium analyses. In the calculations the unknown amounts of carbonate and bicarbonate ions can be replaced by well-known Ca concentrations. No other cations need be taken into account.

The surplus alkalinity, Alk_X

An approximate alkalinity value may be computed as the sum of two parts, one derived from Atlantic water, the other equivalent to the excess of calcium, i.e., the difference between the Ca content of Baltic and oceanic water. The quantity so defined may be called *minimum alkalinity* or Alk_{min}. Combining equations (1) and (2) with (3), (4), and (5) we get the following three equations for calculating the minimum alkalinity:—

Baltic bottom water..... Alk_{min} meq/kg $= 1{\cdot}130 + 0{\cdot}060$ Cl $^0/_{00}$ .... (6)

Baltic surface water ..... Alk_{min} meq/kg $= 0{\cdot}413 + 0{\cdot}232$ Cl $^0/_{00}$ .... (7)

Gulf of Bothnia, all depths . Alk_{min} meq/kg $= 0{\cdot}095 + 0{\cdot}331$ Cl $^0/_{00}$ .... (8)

The difference between the minimum alkalinity, which is a function of the chlorinity, and the actual alkalinity, found by analysis, will be called *surplus alkalinity* or Alk_x. In Table 1 Alk_{min} and Alk_x are found in columns 4 and 5. In Figure 2 the values of Alk_{min} are found to the left of those of Alk_{obs}. The horizontal distances between the two curves are thus equal to Alk_x. In computing Alk_{min} for the Baltic samples the surface equation (7) was used down to the salinity discontinuity at 60 m, from then on the bottom equation was applied.

Table 3

Mean values of Alk_x, the surplus alkalinity, in milliequivalents per kilogramme of sea water at the 8 stations

Gulf of Bothnia:				
	F12	F25A	F29	F64
0 m – bottom.....	0·072	0·066	0·064	0·060
Baltic:				
	F72A	F78B	DBS8	DBS5
0 m – 60 m.....	0·115	0·088	0·100	0·109
80 m – bottom.....	0·148	0·158	0·129	0·166

In considering the values of the surplus alkalinity one must bear in mind that all the various analytical errors enter in full into these values, though the errors may in part compensate each other. It is, therefore, not surprising that the values are uneven. Not too much importance should be attached to the single values, but we should rather pay attention to the general picture which they present. Several interesting conclusions can be drawn of which the first is that the surplus alkalinity is not a function of the chlorinity. Table 3, which gives mean values of Alk_x at the different stations, takes us a step further.

It is seen that in the Gulf of Bothnia with its homogeneous water the mean surplus alkalinity is low and almost constant with a slight decrease towards the south, whereas in the Baltic proper the values are higher and there is a distinct difference between the surface and the bottom layers. Considering now conditions at the separate stations, we see from Figure 2 that in the Gulf of Bothnia there is a more of less pronounced decrease towards the bottom starting from a small increase at 40 or 60 metres. The decrease is most marked at F64 and especially noticeable when we compare the bottom value there with those at the three other stations. Thus when proceeding from north to south and from surface to bottom, the surplus alkalinity gradually disappears. At the bottom of the water column at F64, the southernmost and deepest station, it has actually vanished and the minimum alkalinity here accounts for the whole of the alkalinity found by analysis. The small negative value of Alk_x at the bottom lies quite within the analytical error. The surplus alkalinity does not disappear without leaving some traces. In his work on the carbonic acid balance in the Baltic, Buch (1945) calculated mean values for the 8-year period 1927–1935 partly of observed, partly of calculated data for the Finnish hydrographical stations. Among the latter were the total carbon doixide, $\Sigma\ CO_2$, the excess carbon dioxide $\Delta\ CO_2$, and the carbon dioxide tension p CO_2; $\Sigma\ CO_2$ is the sum of the carbonate ions, the bicarbonate ions, and the free dissolved carbon dioxide, $\Delta\ CO_2$ the carbon dioxide present in excess of the amount the water would contain if it were in equilibrium with the atmosphere; this quantity is intended as a measure of the net CO_2 production in the sea. In Table 4 the values for $\Sigma\ CO_2$, $\Delta\ CO_2$, p CO_2 and the O_2 percentage of saturation, are taken from Buch's data for station F64.

We see that the decrease of the surplus alkalinity is accompanied by a small decrease of the O_2 percentage and by a steady increase in $\Delta\ CO_2$, $\Sigma\ CO_2$, and p CO_2. The comparison of Alk_x with $\Delta\ CO_2$ is particularly suggestive since both are of the same order of magnitude. The inference is that there is a connex-

Table 4

Comparison of Alk_x, the surplus alkalinity, with Buch's (1945) data for station F64

Depth	0	20	40	60	80	100	150	200	250	275 m
Alk_x	0·09	·08	·08	·08	·08	·07	·05	·05	·02	·00 meq/kg
ΔCO_2	0·00	0·1	·03	·03	·03	·03	·04	·04	·05	·06 mmol/l
ΣCO_2	1·18	1·22	1·39	1·44	1·47	1·48	1·51	1·52	1·55	1·55 mmol/l
$p\,CO_2$	3·2	4·3	5·4	5·6	5·9	5·9	6·9	7·6	8·7	8·9 atm. $\times 10^{-4}$
O_2	99	95	–	90	–	90	–	87	–	82 % saturation

Table 5

Comparison of Alk_x, surplus alkalinity, for stations F78B with Buch's (1945) data for F78

Depth	0	20	40	60	80	100	150	200 m
Alk_x	0·083	·097	·086	·086	·163	·159	·150	·142 meq/kg
ΔCO_2	0·00	·00	·01	·07	·25	·24	·25	·26 mmol/l
ΣCO_2	1·36	1·43	1·48	1·54	1·81	1·84	1·87	1·87 mmol/l
$p\,CO_2$	2·8	3·4	4·5	10·5	37	36	38	38 atm. $\times 10^{-4}$
O_2	98	–	–	90[1])	–	21	20	20 % saturation

Depth	250	300	350	400	425 m
Alk_x	·164	·165	·153	·160	·163 meq/kg
ΔCO_2	·26	·25	·26	·25	·25 mmol/l
ΣCO_2	1·88	1·88	1·88	1·86	1·87 mmol/l
$p\,CO_2$	39	38	38	37	37 atm. $\times 10^{-4}$
O_2	–	21	–	–	19 % saturation

[1]) Refers to 50 m.

ion between the surplus alkalinity and the carbonic acid constituents and that, consequently, Alk_x is organic in origin.

We cannot expect to find quantitative relationships since the data compared do not refer to the same series of observations. Nor can Alk_x be supposed to be the only organic constituent of sea water subject to oxidation.

In the Baltic proper the surplus alkalinity presents quite a different picture of which station F78B gives a characteristic example. In the surface layer down to 60 m Alk_x varies between 0·083 and 0·097 meq, in the whole of the remaining water column, from 80 to 425 m, between 0·142 and 0·165 meq/kg, thus in both water masses between narrow limits. At stations F72A and DBS8 there is a minimum at 60 m, which would perhaps have been less accentuated if at this lower limit of the surface layer an intermediate equation for the calcium content had been used. Even so, it can be maintained that in the Baltic proper the surplus alkalinity does not show any tendency to disappear; in the deep water there is, if anything, a slight increase towards the bottom. For an understanding of the special conditions in the Baltic proper we turn again to BUCH's work (1945). In Table 5 are found the same data for station F78, not far situated from F78B, as in Table 4 for F64.

We see that all quantities listed in Table 5 undergo a radical change between 60 and 80 m: Alk_x is almost doubled, ΔCO_2 and $p\,CO_2$ are more than trebled and ΣCO_2 increases by 17·5%. From 80 m to the bottom conditions remain stationary but for small fluctuations. The decisive factor is the oxygen supply.

Oxidation goes on in the surface layer as is seen from the moderately increasing values of Δ CO_2, Σ CO_2, and p CO_2. This is paralleled by a small decrease in Alk_x, illustrated more clearly, as already pointed out, at stations F72A and DBS8. At the lower limit of the surface layer the water is still saturated with oxygen to about 90%. Below 80 m, however, the water contains only about 25% of this amount and from 100 m to the bottom the saturation percentage remains at about 20%, i.e., no or only a slight further oxidation takes place. According to BUCH, conditions are practically the same within the whole of the Baltic deep-water mass. The remarkable change taking place below 60 m, notably in the oxygen content, is not due to intense oxidization at this level, but to the fact that the deep water is practically isolated from the surface layer. Organic matter accumulates in the deep and is consumed only in the measure that oxygen, brought chiefly by horizontal movements within the water mass, is available. An equilibrium has established itself characterized by practically constant concentrations of the carbonic acid constituents and oxygen. BUCH (1945, pp. 144 and 146) sums up the situation by stating that the Baltic deep water evidently contains "more oxidizable matter than there is oxygen to oxidize it", whereas in the Gulf of Bothnia there is much less organic matter and more than enough oxygen.

The surplus alkalinity fits perfectly well into the above picture and it seems to the author that there is only one possible conclusion: *the surplus alkalinity is in itself an organic constituent of sea water*. Thus, in spite of the quite different hydrographical conditions, the variations of the surplus alkalinity in the Gulf of Bothnia and in the Baltic proper have led to the same conclusion as to its character.

As was pointed out earlier and as is seen from Table 1 and Figure 2 the alkalinity decreases at the bottom of the water column at stations F25A, F29, and F64. Since WATTENBERG (1933) in his work on the solubility of calcium carbonate in sea water had shown that Atlantic water, down to 100–500 m is oversaturated with respect to $CaCO_3$, and that the alkalinity decreases when carbonate is precipitated—chemically or biologically—it has been considered that precipitation or solution of calcium carbonate are the only factors which can bring about a change in the alkalinity, as expressed by the Alk/Cl value (KOCZY, 1956). Such an explanation, however, is not valid for the bottom water in the northern Baltic, BUCH (1945, p. 202) as well as the author (GRIPENBERG, 1937, p. 172) having shown that the deep water is always undersaturated with respect to calcium carbonate. The oxidation of Alk_x in water rich in oxygen offers, on the contrary, a simple explanation. If the chlorinity remains constant within a water mass, or nearly so, then the minimum alkalinity, which is a chlorinity function, also remains constant; consequently, if Alk_x diminishes, the alkalinity must diminish too. It is probable that oceanic water also has a certain surplus alkalinity, though this is more difficult to define than its Baltic counterpart, and that the small fluctuations observed in the Alk/Cl value in the water masses of the oceans at least in part should be ascribed to fluctuations in the surplus alkalinity, i.e., in the organic content of the water, the surplus alkalinity forming a part of the latter.

Though the author does not maintain that the surplus alkalinity stands for the whole of the organic matter in Baltic water, it may perhaps serve as a rough measure thereof. It has the advantage of being readily accessible to analysis.

The role played by boric acid

Though the comparison with BUCH's carbonic acid data has thus led to the conclusion that the surplus alkalinity is organic in origin, it is not necessary to assume that it consists entirely of anions of weak organic acids. When comparing the few analyses of boric acid, made in connexion with the electrometric alkalinity titrations, with the corresponding values of Alk_X it is seen that in the Bothnian surface water and in the Baltic surface and bottom water both quantities are of the same order of magnitude and in three cases (F78B, 0 m, DBS5, 0 and 105 m) even identical within the analytical errors. This suggests that there may be a connexion between the surplus alkalinity and the boric acid concentration. Now it is a well known fact, on which also the analysis for boron is founded, that boric acid easily forms complexes with organic oxy-compounds, such as carbohydrates. Acids are formed which are stronger than the simple boric acid, but are still weak acids. BUCH (1945, p. 137) concluded from the mean ratio of Δ CO_2 to Δ O_2*) in Baltic deep water (Δ O_2 being defined as the difference between the oxygen saturation value and the actual oxygen concentration, both in mmol/l) that the dissolved organic matter consists mainly of substances having the character of carbohydrates. It is therefore possible that Alk_X is not formed directly of anions of organic acids, but rather of organic decomposition products coupled with boric acid. If this is true, the boric acid present in the water may become wholly or partly titrated already in the alkalinity analysis though it is not recognized as such, but is included in the alkalinity value. In the measure that the dissolved organic matter becomes oxidized, as in the deep water at station F64, the boric acid is gradually liberated from its organic appendage and goes back into its ordinary state. It is therefore obvious that complicated conditions may prevail near and at the equivalence point in the alkalinity titration and these conditions may vary from sample to sample, depending on the state of oxidation of the organic matter and on how much of the boric acid becomes co-titrated. The equivalence point will depend upon whether the water contains the simple boric acid, a stronger complex acid, or both. As a matter of fact, small unevennesses in the electrometrical titration curves, both before and after the equivalence point, were often observed. These were taken as technical imperfections and were levelled out in the interpolation for the equivalence point, but some of them may actually have been secondary equivalence points. The lack of adjustment of Baltic alkalinity values to a strictly linear relationship to the chlorinity may find its explanation in these circumstances and especially in the fact that the surplus alkalinity is not a chlorinity function. The boric acid analysis may be less influenced since so much mannitol is added in this analysis that the boric-acid-mannitol complex may prevail over already existing combinations.

GAST and THOMPSON (1950) have shown that the boric acid concentration of sea water increases when the water is treated with permanganate in acid solution. They present analyses of the boric acid content before and after oxidation in 32 samples from 2 stations, one in the north-east Pacific, the other in Puget Sound. The increase in the boron content varied from zero to 0·015 meq. They conclude that part of the boric acid contained in the water was combined with polyhydroxy organic matter before the oxidation and thus inaccessible to

*) The ratio is compared with the *respiratory quotient*, RQ, used in physiology.

combination with the mannitol added in the analysis. The results are given as mmols of polyhydroxy organic matter per litre (twice the amount as meq). The authors assume that the organic boric acids—like the mannitol boric acid—are much stronger than the simple boric acid and therefore titratable with sodium hydroxide in the alkalinity back titration. This results in a lower alkalinity value than would have been obtained if the water had not contained organic boric acid complexes. Such a conclusion cannot be drawn from the Baltic material. In the Baltic the organic boric acids, though stronger than the simple boric acid, must still be weak acids, or, in other words, in the electrometric back titration the equivalence point which coincides with the inflection point of the titration curve, must occur before the organic acids have been titrated. Otherwise one cannot explain that in the Gulf of Bothnia the decrease of the alkalinity in the depth—where the chlorinity is practically constant—is accompanied by a decrease of the surplus alkalinity. If the conclusion of GAST and THOMPSON were valid the opposite should be the rule. This is an important point which further work must clarify. The work of GAST and THOMPSON which has been confirmed by NOAKES and HOOD (1959), who even obtained higher organic borate values, is of utmost importance since it draws the attention of scientists to the significant connexion between the alkalinity, the organic matter, and the boric acid concentration of sea water and shows that the problem of the organic matter content can be attacked from new angles. It has an important bearing also on the conditions governing the precipitation of calcium carbonate in the sea. The notion of the surplus alkalinity in the Baltic, arrived at from an entirely different point of view, may contribute to amplify the picture.

The division of the alkalinity into two parts, the minimum and the surplus alkalinity, was originally prompted simply by a wish to separate the known from the unknown and by studying the variations of the unknown to gain some information on its nature. It is the hope of the author that the conclusions arrived at may serve as a working hypothesis for further investigations.

Summary

Sixty-five alkalinity and thirteen boric acid analyses of Baltic water are presented. A new way of treating the material is proposed founded on three well established relationships: (1) that between the alkalinity and the chlorinity in oceanic water, (2) that between the Ca concentration and the chlorinity in oceanic, and (3) in Baltic water.

A quantity called *minimum alkalinity* is defined. This is composed of two parts, one derived from the alkalinity of the oceanic fraction of the water, the other from the excess calcium, i. e., the difference between the calcium content of Baltic and oceanic water. This part is due to dissolved carbonate brought down by rivers.

Three equations, (6), (7), and (8) are computed, valid for the bottom and surface water of the Baltic proper and for water of all depths in the Gulf of Bothnia.

The difference between the alkalinity found by analysis and the minimum alkalinity is called *surplus alkalinity* or Alk_x. Alk_{min} and Alk_x are found in columns 4 and 5 of Table 1. In Figure 2 the curve for Alk_{min} lies to the left of Alk_{obs}. The horizontal differences between the two are equal to Alk_x. It is

concluded from the variations of Alk_x in the Gulf of Bothnia and in the Baltic proper compared with those of certain carbonic acid constituents, $\Sigma\ CO_2$, $\Delta\ CO_2$, and p CO_2, as calculated by BUCH (1945), that Alk_x is in itself an organic constituent of the water. It is, however, recognized that Alk_x may not be made up directly of anions of weak organic acids, but rather of organic decomposition products forming complex anions with boric acid.

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An Inductive Salinity Meter for *in situ* Measurements

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Introduction

This instrument is designed to measure the salinity and temperature of the sea *in situ*, by means of a conductivity and temperature measurement. The instrument is in two units, one being used on board a ship, and the other unit is lowered from the ship, being connected to it by a four conductor cable. An induction type probe is used which forms part of an A.C. bridge working at 1·3 kc/s. The advantage of this method of measurement, resulting from elimination of electrode troubles, has been realized for some time (ESTERSON, 1957; HINKELMANN, 1957).

If the A.C. bridge is used on deck and connected to the underwater unit through a cable, the impedances of the cable will introduce errors which limit the length of cable which can be used.

This difficulty is overcome by placing the whole A.C. bridge in the underwater unit with the probe. The bridge is balanced by driving a potentiometer with a small electric motor and reduction gear. The motor is controlled manually from the surface, and the signal from the bridge when off balance can be heard on the surface in headphones. When the bridge is balanced, the balance position is determined from the surface by measuring the resistance of the part of the potentiometer in circuit by means of a Wheatstone Bridge on the deck. Errors introduced by the cable are much less when D.C. measurement is used, and they can be corrected if necessary. The Wheatstone Bridge is also used to determine the *in situ* temperature by measuring the resistance of a thermistor in contact with the sea water.

Description

Underwater unit (Figs. 1 and 2)

The underwater unit is housed in a bronze cylinder with cast iron end plates, sealed with O-rings. All metal parts are protected by corrosion-resisting paint.

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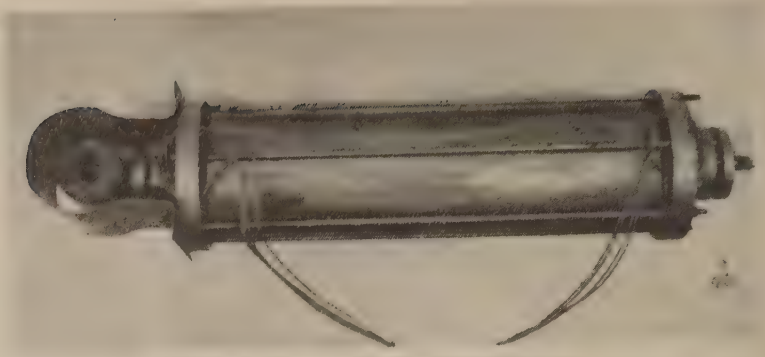

Figure 1. Photograph of the underwater unit.

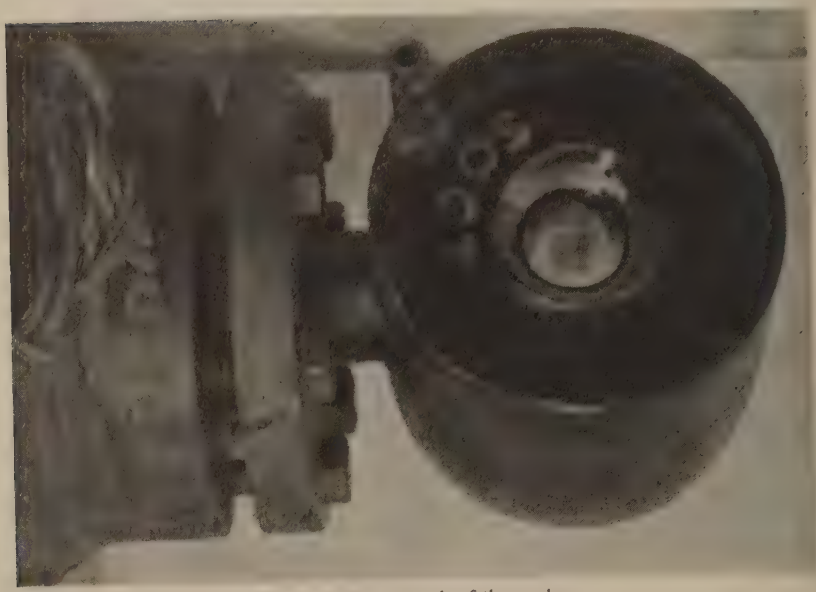

Figure 2. Photograph of the probe.

The probe has a stem which passes through a seal at one end of the housing, and the connecting cable passes through a seal at the other.

The probe is protected by a metal shield arranged so as to minimize its effect on the electric field in the water. A further seal is provided with feed-throughs, to prevent water entering the instrument in the event of damage to the cable. Silica gel is used to keep the interior dry. The underwater unit is 2′ 3″ long (69 cm), 6″ in diameter (15 cm), and weights 55 lb (25 kg).

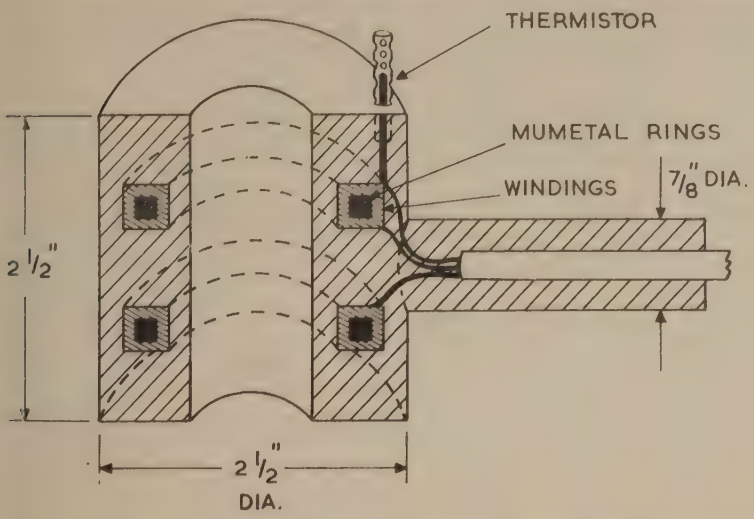

Figure 3. Diagram to show the construction of the probe.

(1) The probe (Fig. 3)

The probe unit consists of two mumetal rings with toroidal windings. They are cast in an Araldite block in such a way that, when immersed, a sea-water conduction circuit exists in the form of a one turn loop which passes through both the rings. The thermistor element is enclosed in a glass tube, one end of which is set in the Araldite so that the sensitive end is in contact with the sea water, and is protected from damage by a perforated brass tube.

(2) Underwater oscillator, bridge, and amplifier (Fig. 4)

The resistance of the sea-water circuit forms one arm of the bridge, and the resistance of part of the potentiometer (VR1), together with R15, forms the other arm. One mumetal ring has an energizing winding (W1, 50T) which is fed from an oscillator.

The other ring has a detector winding (W2, 45 turns) which is connected to the detector amplifier. Both rings have balancing windings (W3, W4, 5 turns each) which are connected so that the fluxes in the second mumetal ring due to the currents in the sea water and the potentiometer tend to cancel. Balance of the bridge is achieved when the ratio of the potentiometer resistance in circuit + R15 to the resistance of the sea-water circuit is the square of the turns ratio. The turns ratio is 5:1, 5 turns in the balancing windings, and one in the sea-water circuit. There is also a single turn winding on both rings (W5, W6) which is connected to a small fixed capacitor (C8). C8 and trimmer VC1 enable any reactive coupling to the detector winding to be balanced out.

It would be unsatisfactory to feed the bridge from an oscillator on the surface because of the likelihood of crosstalk in the cable between the conductors carrying the signal from the oscillator, and those carrying the out of balance

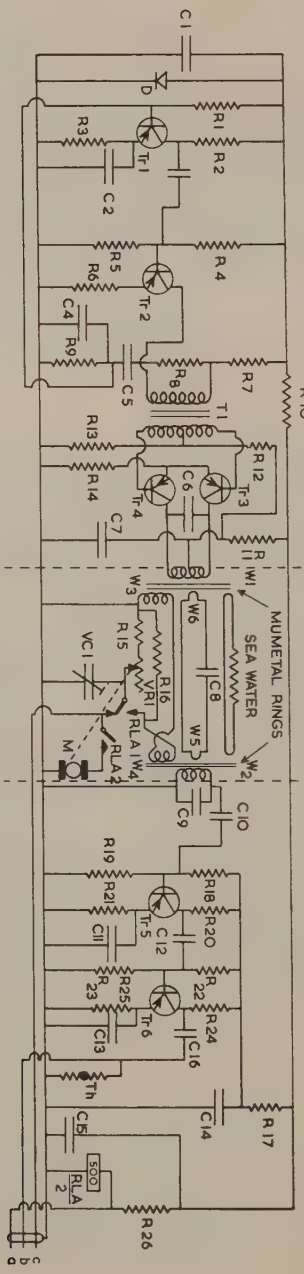

Figure 4. Circuit diagram of underwater unit. Components are listed on p. 31.

signal from the bridge to the surface. For this reason the oscillator is placed below with the bridge, and fed with D.C. from the surface. The D.C. supply is switched off while D.C. measurements are being made, to avoid errors due to voltage drop in the cable.

Transistors are used throughout as they simplify power supplies, save space, and are more robust than valves.

After balancing the A.C. bridge, the potentiometer (VR1) is connected in the D.C. bridge by means of a relay.

The oscillator consists of a two-stage amplifier with feedback through a Wien Bridge network (R8, C5, R9, and C4). The gain of the amplifier is limited by using a comparatively low collector load resistance (R7) to provide the feedback voltage.

The D.C. supply to the oscillator is stabilized by a zener diode (D). Good decoupling is required to prevent coupling between the oscillator and amplifier through the common D.C. supply.

The signal from the oscillator is amplified by a push-pull amplifier, which supplies the centre-tapped 50 turn energizing winding (W1) on one mumetal ring. A fixed resistance (R15) is connected in series with the potentiometer (VR1), and this could be altered if necessary to measure abnormal conductivities. The potentiometer (VR1) is a 10 turn helical potentiometer with high resolution. To cancel unwanted resistive coupling due to stray magnetic fields, a resistor (R16) is connected in the balancing circuit. This is 1·8 Megohm in the prototype. The value of this resistor is determined by adjusting it so that the bridge is balanced with the probe in air (zero conductivity) and the potentiometer VR1 open circuited.

A plot of the reciprocal of the balancing resistance in circuit against the reciprocal of the resistance of the sea-water circuit should therefore be a straight line passing through the origin. The value of R16 is sufficiently high for temperature effects on it to be unimportant. Similarly, capacitors C8 and VC1 are sufficiently small for temperature effects to be unimportant.

The effect of temperature on R15 and VR1 is unimportant, because the resistance in circuit is measured immediately after balancing the A.C. bridge.

The detector amplifier is a conventional two-stage R. C. coupled amplifier. The input is tuned with a 0·5 μF capacitor (C9) which helps to reduce harmonics. The output from the amplifier is coupled via a 0·5 μF 250 volt paper capacitor (C16) to the conductor (b) which carries the signal to the deck unit. For economy of conductors this conductor is also used for measurement of the resistance of the thermistor, to determine the sea-water temperature. C16 is a paper capacitor, as an electrolytic here would cause errors in the D.C. measurement. C17 in the deck unit is a paper capacitor for the same reason. A small permanent magnet electric motor is used to drive the potentiometer VR1 through a 1000:1 reduction gear. A friction drive is provided to avoid overdriving the potentiometer if the slider reaches the end stop. The live conductor which is used to supply the motor is also used for D.C. measurement of the potentiometer resistance. This gives further economy of conductors, and is achieved by making the appropriate connextions at each end of the cable with relays, RLA and RLB. A third conductor supplies 12 volts D.C. for the oscillator, amplifier, and relay in the underwater unit. Earth return via the cable screening is used for the D.C. supplies, for the A.C. signal, and for D.C. measurements.

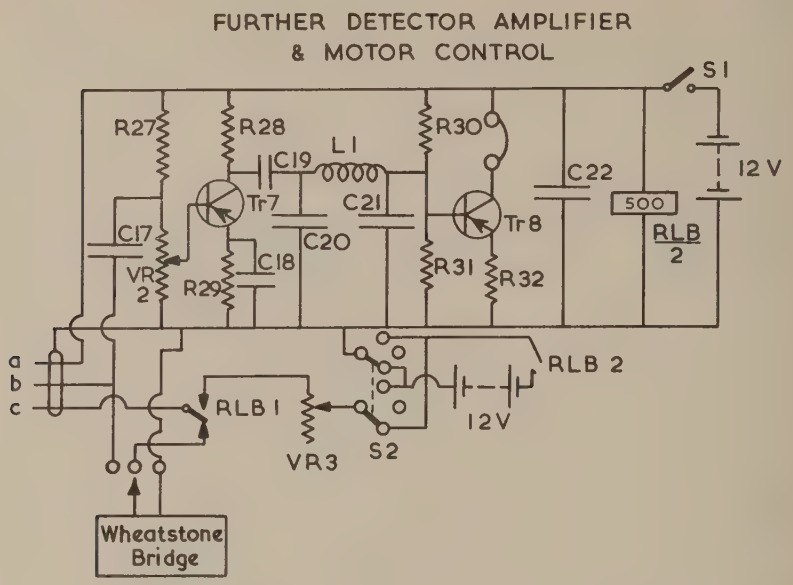

Figure 5. Circuit diagram of deck unit. Components are listed on p. 31.

Deck unit (Fig. 5)

The deck unit consists of a further two-stage amplifier feeding a pair of headphones, and the motor control unit. These are housed in a small wooden box. A portable Wheatstone Bridge is also required, and two small 12 volt batteries to power the instrument. The current consumption is 120 mA intermittently. The deck amplifier incorporates a manual gain control and a *II* section low pass filter to attenuate harmonics. The motor is fed from one 12 volt battery via a reversing and on/off switch, and a resistance speed control. The other battery supplies the transistor circuits and relays.

Calibration

For calibration the instrument was suspended in the centre of a 100-gallon asbestos tank of sea water, with provision for heating, cooling, and stirring. If a metal tank were used, the conductivity might be altered by dissolved salts from the metal. A large tank is necessary, as the close proximity of objects is liable to alter the conductivity reading. A precision mercury thermometer was partly immersed in the tank, and a periscope arranged to read it.

At frequent intervals during the calibration samples of sea water were taken from the tank. The salinity of these samples was determined by precision conductivity measurements. Although no fresh water was added to the tank, several salinity determinations are necessary, as the salinity will increase slightly due to evaporation. The range of conductivity required was obtained by varying the temperature only.

The sea-water temperature was varied over a wide range, and readings were taken at approximately half degree intervals of temperature, thermistor resistance, and potentiometer resistance, after balancing the A.C. bridge. The heater or refrigerator was switched off a few minutes before taking each set of readings to allow the temperature to become steady. The stirrer was running continuously. All resistance readings were corrected for errors in the Wheatstone Bridge and for cable resistance. All temperature readings were corrected for thermometer errors by comparing the thermometer used with an NPL calibrated thermometer. The conductivity was calculated in each case from the temperature and salinity using Admiralty publication H.D. 481, based on the work of THOMAS, THOMPSON, and UTTERBACK (1934). The general expression for conductivity is of the form: –

$$K = \frac{\text{instrument constant}}{\text{corrected resistance reading}} \times (1 - 9 \times 10^{-5}(T - 10))$$

where T = temperature °C.

The factor in the brackets, derived from the coefficient of expansion of Araldite, is an attempt to correct for the change in dimensions of the Araldite casting with temperature. The expression: –

$$y = \frac{(1 - 9 \times 10^{-5}(T - 10))}{\text{corrected resistance reading}} \text{ Mhos}$$

was plotted against conductivity (see Figure 6). This should give a straight line passing through the origin. The slope of the line gives the instrument constant.

It was found impracticable to check the calibration by a loop of wire and standard resistance connected through the probe to simulate the sea-water. As compared with a non inductive resistor, the sea-water impedance appears to have a phase angle of 0·04° capacitive. This is probably due to eddy currents in the sea water. The trimmer (VC1) is adjusted to give a sharp balance point with the probe in sea water, and the balance point is less sharp when a resistor is used in place of the sea water.

Operation

The underwater unit is lowered from the ship on a rope which passes over a measuring sheave. The electric cable is payed out at the same time, allowing plenty of slack. When the instrument is at the required depth the thermistor resistance is first measured. The A.C. bridge is then switched on, and the electric motor is run until the signal in the 'phones disappears. The sound of the motor can also be heard in the 'phones due to acoustic pick-up in the amplifier. This is useful, as it gives an indication of the speed of the motor, which can thus be easily controlled from the surface. When balanced, the A.C. bridge is switched off, and the potentiometer resistance in circuit is measured on the Wheatstone Bridge. This procedure is then repeated at various depths as required.

The signal in the 'phones gives no indication of which side of balance the

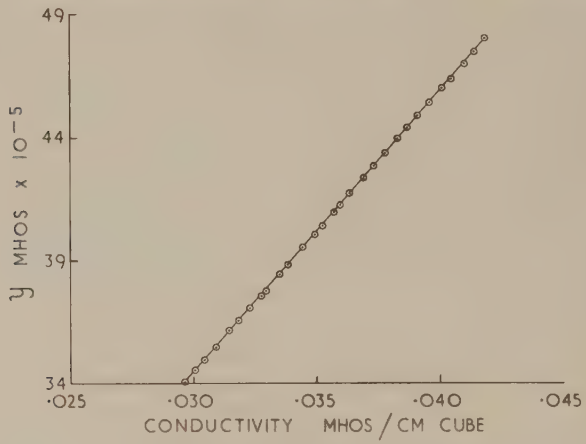

Figure 6. Calibration curve.

bridge is, but the potentiometer resistance has always been found to change in the same direction as the thermistor resistance.

To serve as a warning in the event of sea water getting into the cable and causing electrical leakage, a spare conductor in the cable is left unconnected at the lower end, and the leakage between this conductor and the earth screen is measured with a 500 volt megger at regular intervals.

Calculation of Results

The *in situ* conductivity is given by the expression on page 27. The corrected resistance reading in this expression is obtained by subtracting the cable resistance from the bridge reading. This is also done in determining the temperature. The temperature is obtained by interpolating from the calibration figures. It is necessary to correct the *in situ* conductivity for the effect of pressure on conductivity, to obtain the equivalent conductivity under atmospheric pressure. The data published by HAMON (1958) is used for this. The salinity is obtained from the temperature and corrected conductivity using Admiralty publication H.D. 481.

Results

The results of measurements in the calibrating tank are shown in Figure 6. This is a graph of the quantity

$$y = \frac{1 - 9 \times 10^{-5} (T - 10)}{\text{corrected resistance reading}} \text{ Mhos}$$

against the conductivity of the sea water.

The graph shows that the calibration curve is a straight line passing through the origin, as expected from theory. As the errors are too small to see on this graph, the departures of the individual points from the straight line are plotted

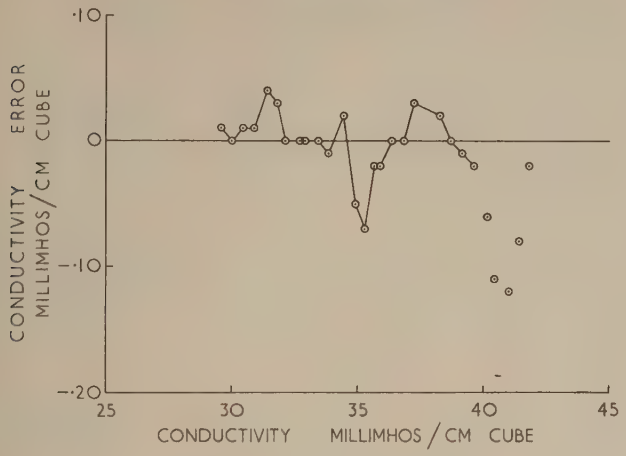

Figure 7. Errors in calibration curve.

in Figure 7. The end five points corresponding to conductivities above ·04 Mhos/cm^3 have not been joined up and are disregarded. They are unreliable due to the formation of air bubbles on the instrument due to the rise in temperature. The remaining points are scattered in a random manner about the straight line given by

$$\text{conductivity } K = \frac{87{\cdot}09}{\text{corrected resistance reading}} \times (1 - 9 \times 10^{-5}\,(T - 10))$$

The average departure from this line corresponds to 0·0000175 Mhos/cm^3 in conductivity, which is about 0·05% of the conductivity. This corresponds to an average salinity error of about 0·015 $^0/_{00}$. These figures include errors in measuring the temperature in the tank with a mercury thermometer, and errors in measuring the salinity. The mercury thermometer is calibrated in 0·05°C divisions, but can be read with care to 0·01°C. The accuracy of calibration of the thermometer is $\pm$ ·02°C.

Errors introduced by temperature measurement with the thermistor are not included in these figures. However, it should be possible to measure temperature with the thermistor to the same order of accuracy as with the mercury thermometer used here, provided the calibration is checked from time to time.

The instrument was used regularly at sea for about two months, at depths down to 150 m*). At the end of this period, however, the temperature calibration suddenly changed by nearly 0·2°C due to a change in the thermistor. Discrepancies of a few metres in the depth measurements were observed on occasions. This is due to stretch of the suspending rope and uncertainty about its angle. On one occasion samples of water were taken with a water bottle, and the salinity was determined independently from the samples. The results are shown in the following table.

*) Maximum depth available.

Depth m	Temperature (from thermistor reading) °C	Salinity (from instrument reading) ‰	Salinity (from samples) (where available) ‰
1	6·45	29·57	–
5	7·30	31·15	30·61
10	8·33	32·30	32·28
20	8·38	32·85	32·81
30	8·68	32·96	–
40	8·89	33·15	33·12
50	8·83	33·22	–
60	9·06	33·40	33·22

The agreement is not as good as one would expect from the results of the laboratory test, but all the discrepancies except possibly the one at 60 m could be explained by a small error in depth measurement.

Advantages

The most important advantage of this instrument is the use of D.C. for measurement over the cable. This makes it possible to use a much longer cable than in instruments where A.C. is used for measurement over the cable. With slight modifications, corrections could be applied for errors due to leakage and resistance in the cable, although such errors are very small with the length of cable at present in use (183 m). It is convenient to use D.C. for the conductivity measurement as it is already required for the temperature measurement.

A further advantage is that there are no precision resistors in the underwater unit. The only precision resistors are in the Wheatstone Bridge on deck, and it is relatively easy to obtain high precision with this type of instrument.

Both the underwater unit and the deck unit are compact and robust, and the power requirements are small (120 mA intermittently from two 12 volt batteries). The instrument should be comparatively inexpensive to make.

Suggested Improvements

It is felt that a much higher accuracy is possible with this technique than has been achieved in the first attempt. The A.C. bridge is basically very simple, and should be capable of high accuracy. To achieve the best possible accuracy, it would be desirable to include a device for balancing the reactive component by remote control. Further amplification of the unbalance signal would be required, together with greater care to avoid unwanted coupling between the oscillator and detector. A fine adjustment of resistance would also be useful.

Provided sufficient conductors are available, the three-wire system could be used to compensate for the resistance of the cable, and the D.C. measuring circuit could be isolated from the earth screen.

It should be possible to build a lighter housing in corrosion-resisting alloy. The underwater unit could be suspended from a strain bearing electric cable.

One could design a special D.C. bridge in which the change of thermistor resistance is used to compensate automatically for the effect of temperature on the sea-water resistivity. The bridge could then be made direct reading in terms of salinity (HAMON, 1956). This would inevitably lose some accuracy, but for some purposes this would be justified by the convenience of obtaining an immediate reading.

Components List

Deck Unit

Resistors fixed

R27	82 K ohms
R28	1 K ohm
R29	1 K ohm
R30	82 K ohms
R31	10 K ohms
R32	1 K ohm

All ¼ watt

Resistors variable

VR2	10 K ohms w.w.
VR3	50 ohms w.w.

S 1 S.P. On/off switch
S 2 2 p. 3 w. Motor switch
2 12 volt batteries (3. A.H.)
Headphones (high resistance)
Wheatstone Bridge

Capacitors

	Capacity	voltage	Type
C17	0·5 μF	250 v	Paper
C18	5 μF	15 v	Electrolytic
C19	5 μF	15 v	Electrolytic
C20	0·2 μF	250 v	Paper
C21	0·2 μF	250 v	Paper
C22	50 μF	15 v	Electrolytic

Transistors

Tr7	OC71
Tr8	OC71

Inductance

L1	200 mH	
RLB	Relay	P.O. type 3000 500 ohm winding 1 changeover 1 make platinum contacts

Underwater Unit

Resistors fixed

R1	1·2 K ohms
R2	2·2 K ohms
R3	1·0 K ohms
R4	39·0 K ohms
R5	10·0 K ohms
R6	1·0 K ohms
R7	330 ohms
R8	330 ohms
R9	330 ohms
R10	470 ohms
R11	150 ohms
R12	3.3 K ohms
R13	100 ohms
R14	10 ohms
R15	1·8 K ohms
R16	1·8 M ohms
R17	1·0 K ohms
R18	27·0 K ohms
R19	8·2 K ohms
R20	1·5 K ohms
R21	1·0 K ohms
R22	27·0 K ohms
R23	8·2 K ohms
R24	1·2 K ohms
R25	1·0 K ohms
R26	33 ohms

All ¼ watt

Resistors variable

VR1	1 K ohm 10 turns helical potentiometer

D Diode (Zener) OAZ203
Th Thermistor S.T.C. Type F23

RLA	Relay	P.O. Type 3000 500 ohm winding 1 changeover 1 make platinum contacts

Capacitors

	Capacity	voltage	Type
C1	100 μF	15 v	Electrolytic
C2	5 μF	15 v	Electrolytic
C3	5 μF	15 v	Electrolytic
C4	0·5 μF	250 v	Paper
C5	0·5 μF	250 v	Paper
C6	1 μF	250 v	Paper
C7	50 μF	15 v	Electrolytic
C8	0·01 μF	–	Mica
C9	1 μF	250 v	Paper
C10	5 μF	15 v	Electrolytic
C11	5 μF	15 v	Electrolytic
C12	5 μF	15 v	Electrolytic
C13	5 μF	15 v	Electrolytic
C14	100 μF	15 v	Electrolytic
C15	100 μF	15 v	Electrolytic
C16	0·5 μF	250 v	Paper
VC1	250 μF		Trimmer

Transistors

Tr1	OC200
Tr2	OC200
Tr3	OC72
Tr4	OC72
Tr5	OC71
Tr6	OC71

M Motor 12 volt permanent magnet

Acknowledgments

I wish to thank Dr. C. H. Mortimer of the Scottish Marine Biological Association, Millport, where this work was carried out, for initiating the work, and for his help and advice throughout the course of development. I am also greatly indebted to Mr. J. S. Craib of Millport, for the design and construction of the underwater housing.

Summary

The main feature of this *in situ* temperature and salinity measuring apparatus is that the A.C. bridge for use with the induction type probe is placed in the underwater unit, and the balance position is transmitted to the surface by D.C. measurement. This avoids the effect of cable impedances on the A.C. bridge. D.C. measurement over the cable is convenient, because it is also used to indicate the temperature by means of a thermistor. Precision resistors are not required in the underwater unit, and D.C. measurement over the cable enables a much longer cable to be used. The accuracy of the first model is estimated to be $\pm$ 0·03 $^0/_{00}$.

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On the Relationship between Primary Production and Standing Stock of Phytoplankton

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Introduction

LOHMANN (1908) was the first investigator to realize the inadequacy of data on total cell concentration for the estimation of the standing stock of phytoplankton. In order to arrive at a true picture of the amounts of plankton present in sea water, he converted his counting results to plasma volumes. LOHMANN's methods involved complicated calculations, and have in general been abandoned in favour of the much simpler process of determining total cell volume. Several workers dealing with marine plankton (e.g., RILEY, 1941, 1957; CUSHING, 1955) or fresh-water plankton (e.g., VERDUIN, 1956; RODHE, VOLLENWEIDER and NAUWERCK, 1958; WRIGHT, 1959) have considered estimates of total cell volume satisfactory for their particular purposes.

It is anticipated (BRAARUD, 1958) that there will be an increasing demand for phytoplankton studies involving counting techniques in conjunction with investigations on primary production according to the ^{14}C method of STEEMANN NIELSEN. Recently, the conversion of counting results to total cell volume values has been recommended (HOLMES, *et al.*, 1958), the implication being that this would facilitate comparisons between the size of the standing stock and the corresponding production values.

There are, however, certain indications that if total cell volume is used as a basis for determinations of standing stock, too much stress will be placed on the large phytoplankton algae in relation to their importance as producers, just as the use of total cell number is likely to cause an over-estimation of small-celled species occurring in large concentrations. RODHE *et al.* (1958) were able to show, with freshwater plankton, that the share in production of the larger algae, i.e., those retained by a plankton net, was in general considerably smaller than their corresponding share in the total cell volume of the populations. These authors apparently used colony size rather than the size of individual cells as a basis for distinguishing the different size categories; it might be

expected that the discrepancy which was noted would have been even larger if this had not been so.

In marine phytoplankton, diatoms frequently constitute the bulk of algae in the large and medium cell size fractions. One conspicuous feature of many planktonic diatoms is the vacuole which, at least in large forms, may occupy a major part of the cell. LOHMANN (1908), in his calculations of plasma volume of diatoms, took particular care to correct his values for the presumably very low content of organic matter in the cell sap. Hence the plasma volumes computed by him mainly represented the thin layer of cytoplasm adhering to the inner cell wall with which the chromatophores are usually associated, in addition to the plasmatic strands traversing the vacuole and supporting the nucleus.

Undoubtedly, in cases where large diatoms form a prominent component of the plankton, only a minor part of the total cell volume of the populations represents photosynthetically active cell substance. In such cases, the relative importance in production of the various species would be represented more closely by their respective plasma volumes than by their cell volumes. An even better solution would be to include in the calculations only those parts of the cytoplasm where the chromatophores are located. The amount of such cytoplasm present in the phytoplankton populations should to some extent depend upon the total cell surface area of the latter. Actually, LOHMANN (1908) observed that the parietal layer of cytoplasm in diatoms usually has a thickness of 1–2 μ. If this is so, total cell surface area, the calculation of which does not offer any greater difficulties than that of total cell volume, may serve as a fairly good estimate of the volume occupied by the chromatophores and the cytoplasm which surrounds them, even when the plankton contains a variety of diatom species.

The present study forms part of a survey of the phytoplankton of the Norwegian Sea in June, 1954. Ecological and biogeographical aspects are being dealt with in a separate paper (PAASCHE, 1960), which also includes a regional comparison between the vegetation and the primary production rates as determined by BERGE (1958). In the following sections are presented some of the quantitative relationships which could be established between cell surface area, cell number, cell volume, and primary production, the purpose of the investigation being an evaluation of the different methods of estimating standing stock size.

Material and Methods

The primary production data were obtained by BERGE as *production capacities* according to a modification of STEEMANN NIELSEN's ^{14}C method (see BERGE, 1958). The production capacity values, expressed as mg C $\times$ 10 ^{7} per litre per lux-hour, were determined on surface samples at a light intensity of 4,800 lux, which was considered sufficiently low to justify the assumption that light was the limiting factor for photosynthesis in most or all algae present (see BERGE, 1958). The relationship between production capacity and standing stock could therefore be considered a relatively simple one, mainly determined by the pigment content of the plankton communities. The final production capacity values were corrected so as to represent gross photosynthesis (BERGE, personal communication).

Table 1

Average cell surface areas and cell volumes of some plankton algae

	Number of cells measured	Surface area (μ^2)	Volume (μ^3)
Diatoms			
Chaetoceros borealis	42	9,000	19,000
Chaetoceros debilis	84	730	1,400
Chaetoceros decipiens	54	2,600	9,700
Chaetoceros densus	58	5,000	7,600
Coscinodiscus centralis	25	103,000	2,400,000
Coscinodiscus excentricus	12	8,600	60,000
Fragilariopsis atlantica	14	650	700
Fragilariopsis nana	20	25	15
Nitzschia delicatissima	50	180	70
Nitzschia seriata	40	2,000	2,500
Rhizosolenia alata	13	14,000	37,000
Rhizosolenia hebetata f. *semispina*	40	10,000	18,000
Rhizosolenia styliformis	60	33,700	210,000
Thalassiosira bioculata var. *raripora*	50	400	600
Thalassiosira gravida	43	1,900	5,500
Thalassiothrix longissima	23	17,400	87,500
Others			
Coccolithus huxleyi	31	125	130
Exuviaella baltica	100	450	700
Gyrodinium grenlandicum	20	700	1,000
Phaeocystis pouchetii	10	25	10

The data on standing stock size were obtained by means of the sedimentation technique. The details of the counting procedure have been reviewed elsewhere (PAASCHE, 1960), but possible sources of error will be mentioned briefly below. Estimates of total cell number per litre were arrived at by adding up the concentrations of the different autotrophic plankton species occurring in each sample. For practical reasons, the corresponding values of total cell surface area and total cell volume per litre had to be calculated on the basis of average specific cell surface areas and cell volumes. These were determined using stereometrical formulae in conjunction with cell dimensions which were established for each species in a combined sediment representing a number of selected samples. In Table 1 are summarized specific cell surface areas and cell volumes for the more common algae. Spines were included only in those species where they are known to contain chromatophores.

There was reason to believe that the standing stock estimates could be considered representative only within rather wide limits of the actual populations present in the sea at the time of sampling. Some sources of error, such as those arising from the procedure of sampling and subsampling (see HOLMES and WIDRIG, 1956; LUND, KIPLING, and LE CREN, 1958) evidently affected the cell volume and cell surface area estimates more strongly than the cell number values. The statistical uncertainties relating to sampling concern primarily those species which occur at relatively low frequencies, but which may still form an important component of the plankton because of their large size. Furthermore, it became evident in the course of the plankton counting that the cell counts obtained for this category of algae were influenced by other sources of error as well. It could be shown that especially some of the *Chaetoceros*

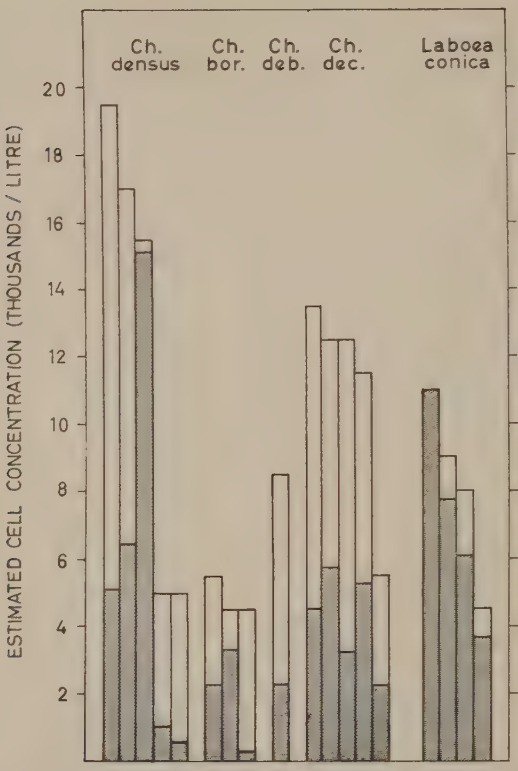

Figure 1. Estimated cell concentrations of *Chaetoceros densus*, *Ch. borealis*, *Ch. debilis*, *Ch. decipiens*, and *Laboea conica* (ciliate) in a number of samples. Estimates based on parallel cell counts in 2 cc cylinders (whole columns) and in 50 cc cylinders (stippled parts).

species did not always sediment completely in the tall 50 cc cylinders in which they were usually counted (Figure 1). Finally, the calculations of specific cell surface areas and cell volumes were clearly subject to considerable error due to the inadequacy of the stereometrical models which were used. Even greater errors probably arose from the application of these average values to populations of atypically small or large cells. In one extreme case it was found that the use of the average cell volume of *Chaetoceros debilis* resulted in an overestimation of the total cell volume of the whole plankton population by as much as 100 per cent.

The total cell number estimates were probably affected little, if at all, by the sources of error just mentioned. In most cases they depended primarily on the concentrations of *Phaeocystis pouchetii* and of small, unidentified flagellates. The difficulties in arriving at correct cell counts for these organisms were enhanced by the circumstance that formalin had been used as a preservative. This reagent is known to destroy some naked flagellates completely, while others are disfigured to such an extent as to make identification very difficult.

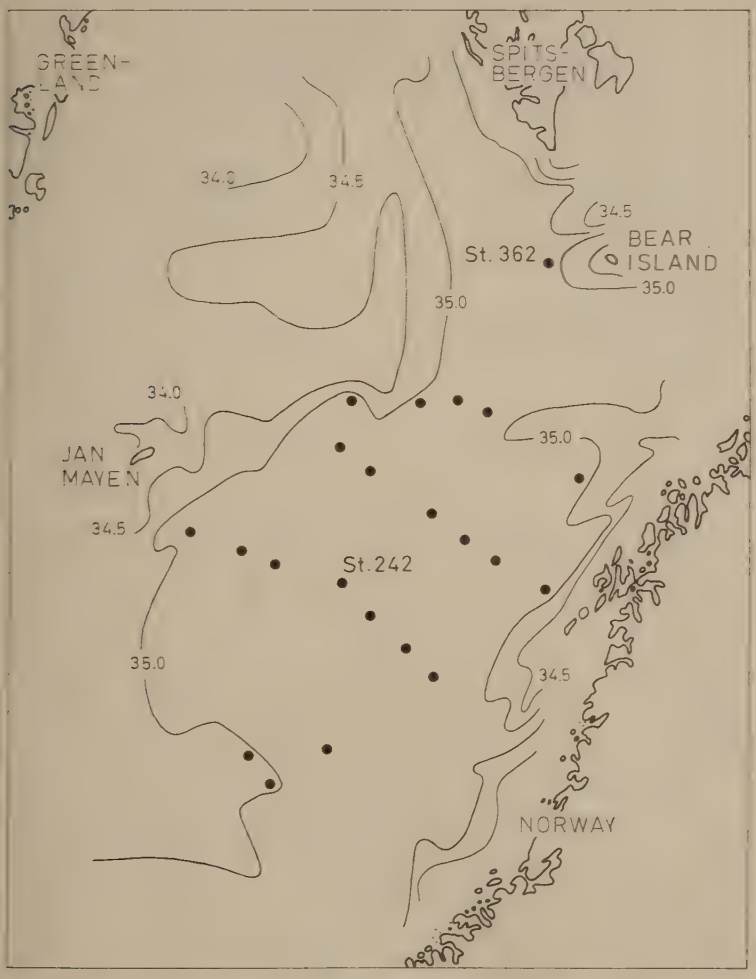

Figure 2. Positions of sampling localities, and isohalines at 20 metres depth according to Eggvin (see Berge, 1958).

The sampling programme included localities in all the main types of water occurring in the Norwegian Sea, and provided a large number of simultaneous observations on production capacity and standing stock. The material at hand therefore permitted correlation and regression calculations using four variables, viz. production capacity, cell number, cell surface area, and cell volume. However, before statistical methods could be applied, it was necessary to subdivide the material according to the gross hydrographical features of the sampling localities, in order to reduce the effect of variations in environmental factors upon the relationship between primary production and size of standing stock. Since it was essential that the plankton populations should comprise the

Table 2

Concentrations of the more important species at two localities
(number of cells per litre of sea water)

	Station 242, 0 metres	Station 362, 0 metres
Diatoms		
Chaetoceros borealis	3,180	260
Chaetoceros debilis	67,500	1,455,000
Chaetoceros decipiens	1,000	320
Chaetoceros densus	10,720	720
Coscinodiscus centralis	320	–
Eucampia zoodiacus	–	14,500
Nitzschia delicatissima	105,000	11,500
Nitzschia seriata	20,000	8,500
Rhizosolenia styliformis	1,580	360
Thalassiosira gravida	2,500	20
Others		
Gyrodinium grenlandicum	46,000	6,500
Phaeocystis pouchetii (including small flagellates)	8,744,000	292,000

whole size range of algae, with both small and large species occurring in significant concentrations, only those relationships which were derived for Atlantic water are presented; in the remaining parts of the Norwegian Sea, the vegetation was predominantly small-celled.

The data used in the present study were obtained from surface samples collected at twenty-two stations, the positions of which are shown in Figure 2. All the stations were located in water with a salinity of 34·95 $^0/_{00}$ or above, and with surface temperatures ranging from 5°C to 9°C. There was very little stratification in the euphotic zone, and nutrient salt concentrations were probably not so low that they formed a serious limiting factor in photosynthesis (see PAASCHE, 1960). The phytoplankton in these waters was fairly uniform as far as the qualitative specific composition was concerned, but the size of the populations and the relative and absolute concentrations of the different species varied widely. This is demonstrated in Table 2 showing the composition of the communities at two stations.

BARNES (1952) has offered several reasons why biological data obtained during field surveys of marine environments should be transformed in some way or other before statistical methods are applied. In the present case a logarithmical transformation was used. This mode of transformation has been employed in investigations of a similar type by TUCKER (1949) and HOLMES (1958).

Results

The scatter diagrams presented in Figures 3–5 are based on log-transformed values of production capacity and standing stock size. Regression lines are included in the diagrams, and the corresponding regression equations are presented in Table 3. The application of a *t* test showed that while the regressions based on cell surface area and cell volume were clearly significant, the significance of the cell number regression was questionable (Table 3).

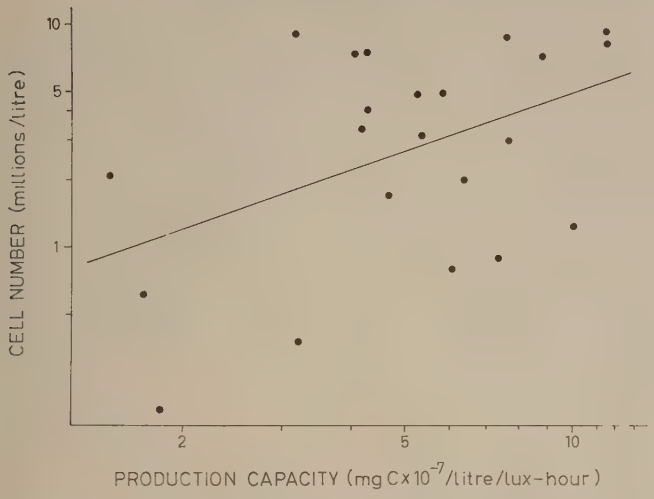

Figure 3. The relationship between cell number and production capacity.

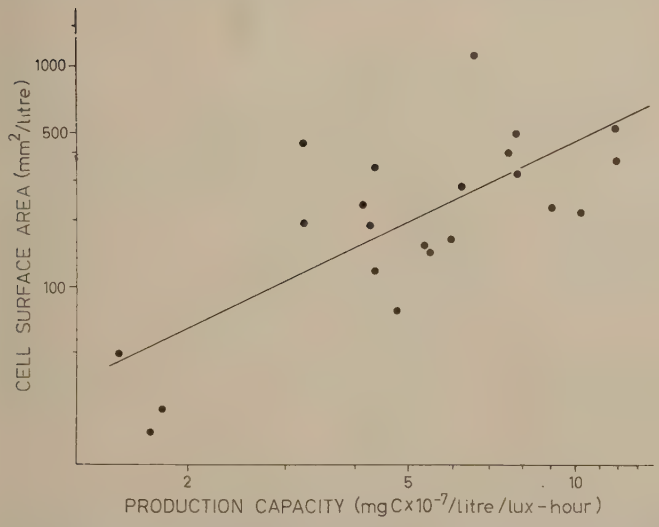

Figure 4. The relationship between cell surface area and production capacity.

Theoretically, a linear relationship is to be expected between non-transformed data on production capacity and standing stock. In the logarithmic scale used, this would mean that the regression coefficients b should not differ from unity. The item $b \pm s_b$ in Table 3 represents the values assumed by b on addition or

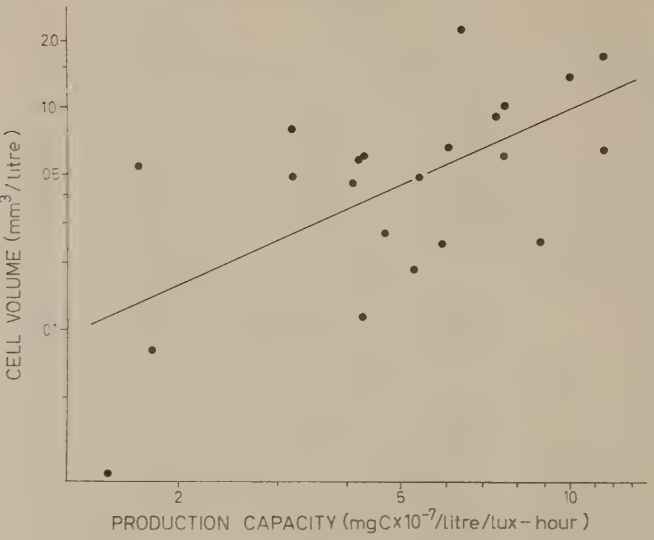

Figure 5. The relationship between cell volume and production capacity.

Table 3

Regression equations for twenty-two surface samples

	Total standing stock estimated as:		
	Cell number	Cell surface area	Cell volume
Units: x =	log production capacity, mg C · 10^{-7} per litre per lux-hour		
y =	log million cells per litre	log mm^2 per litre	log $mm^3 \cdot 10^{-3}$ per litre
Regression equation $y = a + b(x - \bar{x})$....	$y = 0{\cdot}420 + 0{\cdot}865$ $(x - 0{\cdot}699)$	$y = 2{\cdot}299 + 1{\cdot}212$ $(x - 0{\cdot}699)$	$y = 2{\cdot}641 + 1{\cdot}117$ $(x - 0{\cdot}699)$
Probability	0·05–0·02	<0·001	0·01–0·001
$b \pm s_b$	1·250	1·461	1·437
	0·480	0·963	0·797
Standard error of estimate of y.....	0·445	0·288	0·366
Same, re-transformed as % of estimate	+179%	+94%	+132%
	− 64%	−48%	− 57%

subtraction of its standard deviation. An inspection of these values suffices to show that the deviations from unity which do occur are not significant.

The scatter around the regression lines is very considerable, causing large standard errors of estimate (Table 3). An attempt to predict standing stock size from single production capacity values would at most yield an approximate indication of the order of magnitude involved. The question arises whether the present results are at all comparable with those obtained by other investigators using somewhat different methods.

JENKIN (1937) calculated the percentage utilization of incident radiation energy available for photosynthesis in *Coscinodiscus excentricus*. At low light intensities, about 7% of the light falling on exposed cell surface was used. If in the surface area regression (Table 3) the deviation of b from unity is disregarded, the ratio between production capacity and cell surface area is given by the antilogarithm of the difference $(\bar{x} - a)$, which is $2{\cdot}5 \times 10^{-9}$ mg C per lux-hour per mm^2. However, only a fraction of the total cell surface of the populations is simultaneously exposed to light. If all cells were of spherical shape, this fraction would be 0·25 of the total; this value is probably not far removed from the average in any mixed phytoplankton population. Hence, converting to larger units of surface area and light intensity, assimilation in the populations investigated was on the average 1×10^{-3} mg C per kilolux-hour per cm^2 of exposed cell surface. Using the equivalents 1 kilolux = 0·006 g cal per cm^2 per minute (HARVEY, 1957), and 1 mg C = 9·4 g cal, it is found that if the incident energy were to be completely utilized in photosynthesis, the amount of carbon assimilated would be $38{\cdot}3 \times 10^{-3}$ mg C per kilolux-hour per cm^2. Hence the degree of utilization in the populations under investigation was 1/38·3, which is 2·6%. Considering that the methods used are rather different from those employed by JENKIN, the agreement with the value obtained by her seems quite good. At any rate, since the percentage utilization is lower, rather than higher, than the standard set by JENKIN's value, it would seem that the possible failure to recover some of the primary producers in the quantitative samples did not on the whole seriously affect the established relationship between cell surface area and production capacity.

A similar check could be applied in the case of the cell volume regression. STEEMANN NIELSEN and HANSEN (1959) have shown that in temperate surface plankton, the rate of assimilation at low light intensities is about 0·36 mg C per kilolux-hour per mg chlorophyll. In the same way as above for cell surface area, the equation relating cell volume to production capacity (Table 3) is found to correspond to a value of $1{\cdot}14 \times 10^{-3}$ mg C per kilolux-hour per mm^3. According to GILLBRICHT (1952), 1 μg of chlorophyll is contained in 0·139 mm^3 of diatom plankton, which means that 1 mm^3 of such plankton has a chlorophyll content of $7{\cdot}2 \times 10^{-3}$ mg. Therefore, the rate of assimilation per unit of chlorophyll which according to the regression equation was the most likely one at the low light intensities used, was 1·14/7·2, or 0·16 mg C per kilolux-hour per mg chlorophyll. Again, the agreement with the value given by the earlier investigators must be considered quite satisfactory.

The various correlation coefficients which could be derived are presented in Table 4. The probabilities of the coefficients according to a t test are included in the table.

The three coefficients in the first half of the table indicate the degree of mutual dependence present between values of standing stock size obtained by means of the different methods. Actually, bearing in mind the limited number of observations, too much stress should not be placed on the numerical values of the coefficients and the differences between them. But there can be no doubt that the tendency brought out by the coefficients is real. Those small-celled organisms which form the major fraction of a population in terms of cell number contribute very little to its total cell volume, the latter being instead determined primarily by the larger species present. Apparently, in the type of plankton investigated, there was a very low degree of correlation between cell

Table 4

Correlation coefficients for twenty-two surface samples

	Correlation coefficient	Probability
Cell number / Cell surface area	0·50	0·02–0·01
Cell number / Cell volume	0·16	...
Cell surface area / Cell volume	0·72	<0·001
Cell number / Production capacity	0·45	0·05–0·02
Cell surface area / Production capacity ...	0·74	<0·001
Cell volume / Production capacity	0·62	0·01–0·001

number and cell volume. This result was to be expected in view of the fact that the numerical proportion between large and small algae was by no means constant at the different sampling localities. Cell surface, on the other hand, showed a fair degree of correlation with cell number as well as with cell volume. This agrees with the very reasonable assumption that values of total cell surface area rest more evenly on all size categories of plankton algae.

These considerations may be illustrated more specifically using data from one station (242) where the composition of the phytoplankton was in several respects rather close to the average for all the localities investigated. The diagrams in Figure 6 show the relative proportions of the more important species in

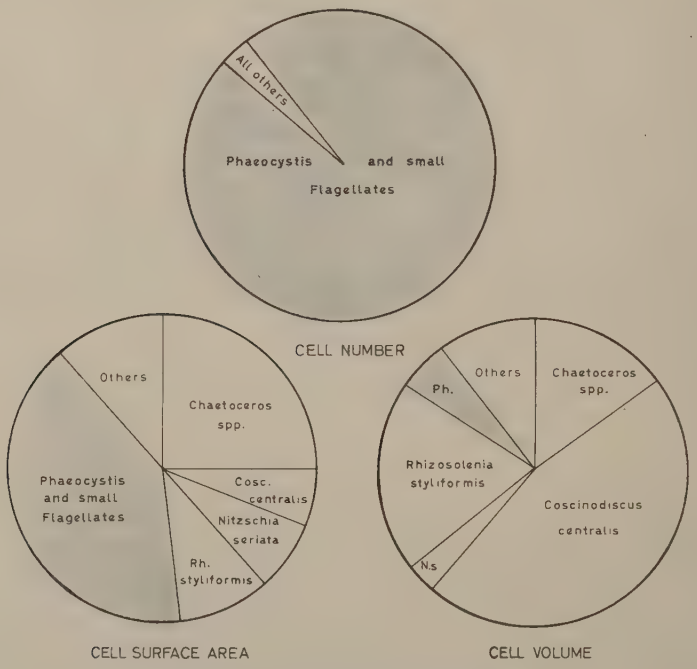

Figure 6. Relative proportion of various species in total cell number, total cell surface area, and total cell volume at station 242.

the total standing stock present, estimated on the basis of cell number, cell surface area, and cell volume, respectively. Numerically, *Phaeocystis pouchetii* and unidentified naked flagellates formed by far the most important fraction of the population. If cell surface was used, various diatoms of medium or large size were about as prominent as *Phaeocystis* and small flagellates. Finally, in terms of cell volume, a major fraction of the total standing stock was accounted for by large diatoms of the genera *Rhizosolenia* and *Coscinodiscus*.

The remaining three correlation coefficients in Table 4 relate production capacity to standing stock estimated according to the respective methods. The highest correlation was present when cell surface area was used as a unit, while the use of cell volume and especially of cell number led to lower correlation values. A result of this kind was to be expected, provided that the reasons presented above for adopting cell surface area as a measure of standing stock of producers are valid. It should be pointed out however, that from a statistical point of view, the differences between the three coefficients may probably just as well be fortuitous. If a larger number of data had been available, and care had been taken to avoid some of the more obvious errors such as those arising from the use of an inadequate preservative, or the use of average specific cell dimensions, it might have been worthwhile to carry the statistical investigation further. By employing statistical methods for testing the possible significance of differences between correlation coefficients, or by applying analogous tests to the corresponding regressions (see WILLIAMS, 1959), it might have been possible to obtain more conclusive evidence in favour of one or the other method of determining size of standing stock.

Discussion

It appears that photosynthesis in phytoplankton shows a high degree of correlation with the chlorophyll content, at least when light intensities are low (RYTHER, 1956b), although a strict proportionality is not to be expected (STEEMANN NIELSEN and HANSEN, 1959). Therefore, if it is assumed that the use of cell surface area is the most adequate method for the estimation of standing stock of primary producers, it follows that the chlorophyll content per unit of cell surface area should be more nearly constant in the different algal species than either chlorophyll per unit of cell volume or per cell.

Starting from data on number of cells per μg chlorophyll in various phytoplankton species, presented by HARVEY (1934), KREY (1939), GRAHAM (1943), and ATKINS and PARKE (1951), and using available information on cell dimensions, calculations were made of cell surface area per μg chlorophyll. The results of these calculations are presented in Table 5. For the sake of comparison, values of cell volume per μg chlorophyll, computed from the same set of data, are included in the table.

The selection of species used requires some comment. Of diatoms on which relevant information is accessible, *Coscinodiscus centralis* and *Nitzschia seriata* are not included in the table. A possible misprint in the original table by ATKINS and PARKE (1951) precludes the use of the data supplied by these authors on *C. centralis*. The form of *N. seriata* studied by GRAHAM (1943) was by him described as "minute", and it seems doubtful whether the average cell dimensions of this species can be used in connexion with the data presented by

Table 5

Number of cells, cell surface area, and cell volume per unit of chlorophyll in some phytoplankton species

Species	Number of cells per μg chlorophyll	Source	Specific cell surface area μ^2	Specific cell volume μ^3	Source for cell dimensions used	Cell surface area (mm^2) per chlorophyll (μg)	Cell volume ($\mu^3 \cdot 10^6$) per chlorophyll (μg)
Diatoms							
Biddulphia regia ..	745 *)	HARVEY (1934)	107,000	2·2 mill.	HUSTEDT (1930)	80	1,640
Rhizosolenia alata	23,500 *)	HARVEY (1934)	14,000	37,000	present invest.	330	870
Thalassiosira gravida	123,000	ATKINS & PARKE (1951)	1,600	4,500	ATKINS & PARKE (1951)	195	550
Chaetoceros vanheurckii ...	170,000	GRAHAM (1943)	1,800	5,430	CUPP (1943)	305	920
Chaetoceros gracilis	286,000	KREY (1939)	220	230	CUPP (1943)	63	66
"*Nitzschia closterium* f. *minutissima*" ..	743,000	ATKINS & PARKE (1951)	35	18	ATKINS & PARKE (1951)	26	13
Others							
Gymnodinium sp.	58,000	ATKINS & PARKE (1951)	700	1,700	ATKINS & PARKE (1951)	40	100
Dicrateria inornata	563,000	ATKINS & PARKE (1951)	50	33	ATKINS & PARKE (1951)	28	19

*) Converted from cells per HPU, using the factor 0·3 HPU per μg chlorophyll (BANSE, 1956).

that author. One dinoflagellate and one chrysophycean are included as a supplement to the more complete set of diatoms listed.

Calculations of the present kind are necessarily subject to considerable error. Nevertheless, the data in Table 5 seem to indicate that there is less variation between species with respect to the ratio between cell surface area and chlorophyll content, than is the case with either of the two other ratios. This is seen most clearly from the range of single values in the respective columns. For cell surface area/chlorophyll, the difference between the highest and the lowest value is about 13-fold, while it is 125-fold for cell volume/chlorophyll and 1000-fold for cell number/chlorophyll. A comparison with the data on cell dimensions shows that, as expected, small species have more cells per unit of chlorophyll than large ones, while conversely large species have more cell volume per unit chlorophyll than small ones. With cell surface area, however, there is no such marked tendency. Clearly, this fact may be interpreted as a confirmation of the assumption that the measurement of plankton populations

in terms of cell number or cell volume leads to over-emphasis of the role played in production by small or large plankton algae, respectively. It is especially noteworthy that in the case of very large diatoms such as *Biddulphia regia*, where the great vacuoles cause very high values of cell volume per unit chlorophyll, the ratio cell surface area/chlorophyll differs but little from that of the smallest phytoplankton species.

Still, judging from Table 5, there seem to exist considerable variations between species with respect to the amount of cell surface area per unit of chlorophyll. Such variations are of course to be expected, since the structural factors which govern the chlorophyll content in the highly differentiated plankton algae presumably are very complex and only in part correlated with the extent of cell surface.

Inter-specific variations in chlorophyll content obviously contributed to the residual variation around all the regression lines, though they may have been of less importance in the surface area regression (Figure 4) than in the volume and cell number regressions (Figures 3 and 5). There are other factors as well which, although they are of a less fundamental order, may have had a similar effect. The chlorophyll content of plankton algae is known to vary intra-specifically within quite wide limits, depending upon environmental conditions such as light intensity (RYTHER, 1956a; STEEMANN NIELSEN and HANSEN, 1959), nutrient salt concentrations (HARVEY, 1953; YENTSCH and VACCARO, 1958), or temperature (MARGALEF, 1954). The importance of these factors in regulating the general interrelationship between photosynthesis and standing stock has on the whole received much attention (e.g., RILEY, STOMMEL, and BUMPUS, 1949). Especially noteworthy are the diurnal variations in photosynthetic capacity which have been shown to result from high light intensities during the day (DOTY and OGURI, 1957); they may be accompanied by short-term variations in chlorophyll content (YENTSCH and RYTHER, 1957). Although little specific information is available, it seems probable that the different species in a plankton community are not influenced in the same way by changes in the environmental conditions, and the effect of the latter on the relationship between the community as a whole and its production capacity is therefore presumably of quite a complex nature.

It is not likely that the data used in the present study were seriously influenced by local or diurnal variations in environmental factors. According to BERGE (1958), light intensities just below the surface in the Norwegian Sea in June 1954 were 7,000 lux or lower, which is very little compared with the intensities needed to produce marked short-term variations in photosynthetic capacity. Although the samples were collected at all hours, the possibility of such variations can be disregarded. As was stated in an earlier section, temperature was rather uniform throughout the sampling area, and nutrient limitation was probably not serious.

The possible proportionality between photosynthesis and cell surface area in large diatoms has several implications which however, with the present state of knowledge, can be the subject of theoretical consideration only. It has been assumed (MUNK and RILEY, 1952), that the degree to which a given nutrient salt concentration of the medium affects the rate of assimilation in diatoms, as measured by the time required for cell division, is primarily determined by the ratio between cell surface area and cell volume. However, in the large and strongly vacuolized diatoms, that part of the cytoplasm in which

photosynthesis is going on might have just as much cell surface at its disposal for the absorption of nutrient salts as would be the case in smaller forms lacking vacuoles. Consequently, they would have the same possibilities as the latter for satisfying those nutritional needs which are immediately linked with the assimilation processes, even when nutrient salt concentrations in the medium are so low as to be generally limiting to photosynthesis. Nor should the nutrient salt concentration of the sea water be more strongly limiting to cell division in the large diatoms, unless there is a specific need for keeping the nitrate and phosphate concentrations in the cell sap on a level more or less corresponding to the nitrogen and phosphorus content of the cytoplasm itself. Whether this is so is still an open question which can only be answered by future investigations.

The fact remains however, that on the whole large diatoms probably have a lower rate of cell division than smaller ones. This is brought out by field observations made by numerous investigators, showing that even during the spring outburst, the larger diatom species always occur in lower cell concentrations than at least some of the smaller algae. The few existing data on division rates under culture conditions (BRAARUD, 1945; LANSKAIA and SIVKOV, 1950) or in nature (MARGALEF, DURAN, and SAIZ, 1955) might possibly be taken to indicate the same phenomenon.

The most likely explanation might be that in large diatoms, a relatively smaller fraction of the energy ultimately deriving from photosynthesis is available for the reproduction of the cytoplasm including the photosynthetic apparatus. GROSS and ZEUTHEN (1948) found that the ionic composition of the cell sap in *Ditylum brightwellii* is probably different from that of sea water. Cyanide, which is known to inhibit respiration, was found to cause plasmolysis in the *Ditylum* cell. If the findings of GROSS and ZEUTHEN are representative, it would seem that in large diatoms, part of the respiratory energy is continually being used for the maintenance and reproduction of the vacuole.

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Summary

1. Phytoplankton samples collected in Atlantic water in the Norwegian Sea in June 1954, were worked up according to the sedimentation method. Standing stock size was expressed in terms of cell surface area as well as of cell number and cell volume. Production capacities had been determined by BERGE, using his modification of the ^{14}C method.

2. Using log-transformed data on standing stock and production capacity, regressions and correlations were calculated for surface samples.

3. The observed relationships between standing stock size and production capacity agreed well with similar observations by earlier authors.

4. The results supported the hypothesis that the total cell surface area of

plankton communities rests more evenly on all size categories of plankton algae than do either total cell volume or total cell number. However, it was not possible to produce conclusive statistical evidence that cell surface area is the most adequate measure of standing stock of primary producers.

5. On the basis of data presented by various investigators, it was demonstrated that the chlorophyll content per unit of cell surface area in a number of phytoplankton species is more nearly constant than chlorophyll per volume unit or per cell.

6. The low division rate of large diatoms was tentatively explained as resulting from a continual expenditure of energy in the maintenance and reproduction of the vacuole.

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Vertical Distribution of Phytoplankton and the Primary Organic Production in the Sea

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Introduction

In our study of the primary production in the Sea of Japan and the Pacific we have found a relationship between the vertical distribution of living phytoplankton and the temperature-density stratification (SOROKIN, 1957). Other authors have also pointed out the existence of such a relationship (GESSNER, 1948; STEEMANN NIELSEN, 1935; SJOMINA, 1957; MOROSOVA-VODJANITZKAJA, 1954; and some others). It is obvious that the vertical distribution of living phytoplankton should influence the rate of primary production at different depths of the euphotic zone and, therefore, the production below 1 m^2. In fact, the rate of photosynthesis changes in the euphotic zone, because of the variations of submarine illumination, caused by the absorption of light in water. It has been shown (STEEMANN NIELSEN and AABYE JENSEN, 1957, and the present paper, see Figure 5) that the maximal rate of photosynthesis in the open sea is usually observed at a depth of 20–30 m. In the upper layer of the euphotic zone, photosynthesis is inhibited by the excess of light. Below this depth its rate decreases because of insufficient illumination and it vanishes at a depth of about 100–120 m. It is obvious, that if the maximum concentration of living phytoplankton occurred at the layer in which the illumination is optimal for photosynthesis, its rate should be maximal. And vice versa, if phytoplankton accumulates in the zone of excess or insufficient illumination, the rate of photosynthesis and of organic production should be much less.

Consequently the determination of primary production under 1 m^2 surface ought to include an accurate determination of the vertical distribution of living phytoplankton. To do this we must know what factors influence the vertical distribution of planktonic algae so as to be able to select appropriate depth for sampling during primary production work. As this point seems to have been largely ignored by previous authors (MIYAKE, 1958; STEEMANN NIELSEN, 1952; JITTS and ROTCHI, 1958; RYTHER, 1956), we have carried out a special study on the problem during an oceanographic expedition in the Atlantic in February–June, 1958.

Figure 1. Station positions.

Methods

We have studied the interrelations between the hydrobiological conditions and the character of the vertical distribution of living phytoplankton at 49 stations in different areas of the Atlantic Ocean and in the Mediterranean (see Figure 1). At every station the samples were taken at the following depths: 0, 10, 20, 30, 50, 75, 100, and 150 m. In these samples the temperature and salinity were determined, and we measured the relative content of living phytoplankton on the basis of its photosynthetic activity under conditions of equal illumination. Before sampling, the vertical temperature stratification in the 0–200 m layer was measured with an electric thermograph. When a thermocline was present additional samples were taken for analysis.

To estimate the relative vertical distribution of living phytoplankton we used the following technique. Samples, taken from various depths, were poured into transparent 0·5 litre bottles and equal volumes, usually 2 ml, of ^{14}C carbonate solution were added to them. The activity of this solution was about $2 \cdot 10^6 - 4 \cdot 10^6$ counts per minute per ml*). The samples were exposed to temperate scattered daylight, for 2–4 hours. The short duration of the experiments helps to avoid the effect of multiplication of algae cells. After the exposure the samples were filtered through millipore membrane filters. After filtration the filters were placed on filter paper and washed with some drops of 2% HCl

*) The working solution of ^{14}C carbonate contained 0·005 M KON and 35 g NaCl per litre. Before use the solution was filtered through a millipore filter.

Table 1

Calculation of K_t, K_r, and K_s factors
A 24 hour station at position 23

Depth m	Vertical distribution of the planktonic algae K_r: Activity of filters after subtracting control counts	K_r	Dependence of photosynthesis rate on submarine illumination K_t: Activity of filters after subtracting control counts	K_t	Vertical distribution of relative rate of photosynthesis $K_s = K_r \times K_t$
0·5	176	1·00	100	1·00	1·00
10	128	0·73	120	1·2	0·87
20	280	1·59	172	1·72	2·73
30	192	1·09	124	1·24	1·35
50	160	0·91	62	0·62	0·56
75	116	0·66	42	0·42	0·27
100	8	0·04	12	0·12	0·0041
150	0	0	0	0	0

in 3% NaCl. The activity of the dried filters was counted under the end-window counter. Two samples, one from upper layer and the other from deeper layer, were used as a control of ^{14}C fixation on filters, which was not connected with the photosynthetic assimilation of CO_2 by algae.

The ratio of the counting rate of each filter corresponding to the samples taken from different depths to the counting rate of the filter from the surface sample are an adequate relative measure of the living algae in these samples, and this ratio is called K_r. In conditions of equal light the amount of living algae in the sample is the main factor acting on photosynthesis rate in so short an experiment. At some stations the dependence of photosynthesis rate on submarine illumination in the euphotic zone, K_t, was also measured. This was determined as the relative rate of photosynthesis in equal samples which were exposed at different depths, usually 0, 10, 20, 30, 50, 70, 95, 120 m. The rate of photosynthesis was analysed as described. In these experiments the main factor influencing the rate of photosynthesis is submarine light. Products of K_t and K_r found for similar depths give a measure, K_s, of the vertical distribution of the relative rates of photosynthesis which actually occur at

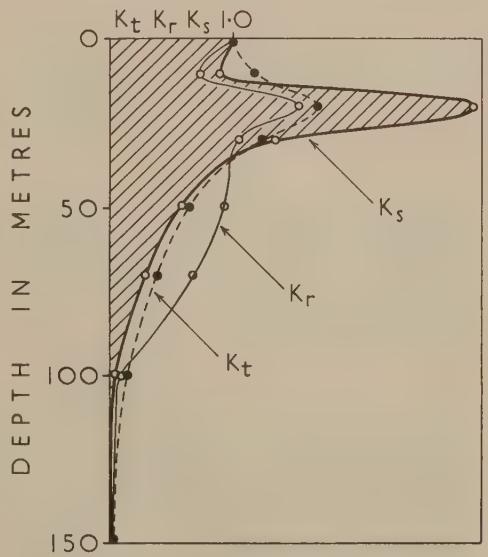

Figure 2. Graphical presentation of data in Table 1.

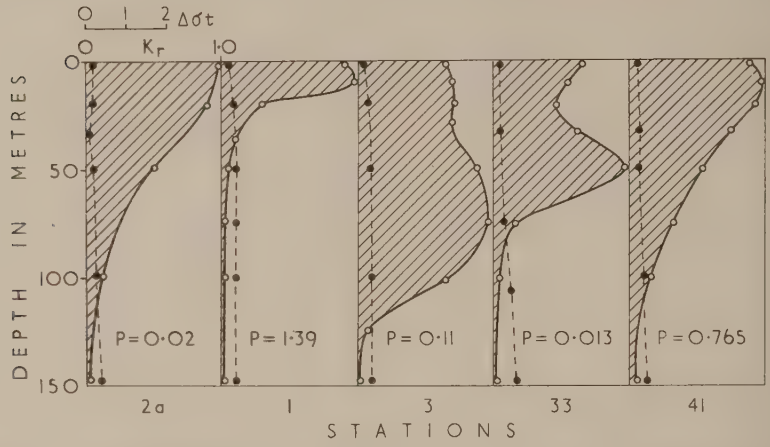

Figure 3. Vertical distribution of phytoplankton in the absence of a thermocline in the euphotic zone.
———○——— = relative phytoplankton distribution, K_r.
———●——— = density change δ_t.
P gives the primary organic production in C g/m²/24 hours.

different depths in the sea (SOROKIN, 1958). Therefore they may serve as the characteristic of the thickness of the productive layer (see Table 1 and Figure 2) and may be used as a basis for calculations of the primary organic production under 1 m² surface. The way in which K_t, K_r, and K_s are calculated from experimental data obtained at Station 23 are shown in Table 1 and graphically in Figure 2, respectively.

Experimental Results

Typical results of the measurements of relative values of the vertical distribution of the living phytoplankton, K_r, are given in Figures 3 and 4. Figure 3 shows the data obtained in the regions of absence of any thermal-density stratification of the euphotic zone. These regions were situated in the temperate waters of the Mediterranean and of the North Atlantic and Canaries Currents, where vertical stratification is absent in early spring. In tropical waters, stations have been worked in the Sargasso Sea, where there is no stratification. In the Sargasso Sea the absence of stratification is caused by constant sinking of warm surface water (SVERDRUP, JOHNSON, and FLEMING, 1946). In Figure 3 it may be seen that in the absence of any noticeable stratification the vertical distribution of the living phytoplankton is approximately homogenous. The amount of living phytoplankton is usually maximal near the surface in the layer of optimal illumination and it falls gradually with the depth. In general, the curves of vertical distribution of phytoplankton, K_r, in such regions are, to some degree, similar to the curves of the dependence of photosynthesis rate upon submarine illumination K_t. This may be, because the rate of multiplication of algae cells depends mainly upon illumination, and other factors which might influence

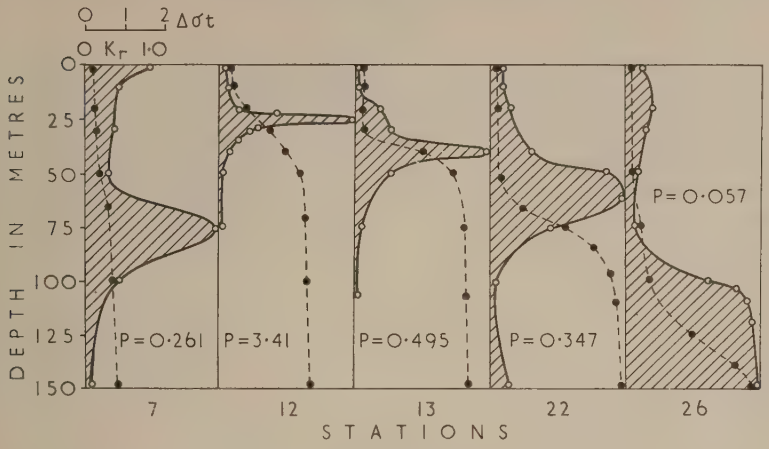

Figure 4. Vertical distribution of phytoplankton in the presence of a thermocline in the euphotic zone.
———○——— = relative phytoplankton distribution, K_r.
———●——— = density change δ_t.
P gives the primary organic production in C g/m²/24 hours.

photosynthesis, excluding light, are uniform. On the other hand, the cells of algae do not find any obstacle, such as change of density, which might prevent their sinking and allow them to accumulate at a particular depth.

We have found quite a different situation in regions where stratification is present, such as in the tropical waters of the North and South Equatorial Current. The results of measurements of the vertical distribution of living phytoplankton, K_r, in these regions are shown in Figure 4. As we may see, even the appearance of a small density gradient, such as 0·5 conventional unit σ_t per 50 m thickness of water layer in the euphotic zone, caused a marked accumulation of phytoplankton. In the case of more clear cut stratification the plankton accumulates much more strongly in the upper zone of thermocline. For example, at stations 12 and 13, near the west coast of Africa, where the upwelling of cold deep water takes place, the water density increases by one σ_t unit per layer of 8–15 m. The content of the living plankton in the layer of thermocline was 30–50 times that in the surface layer. The thickness of the zone of phytoplankton was very small. From Figure 4 it also may be seen that increase in the depth of the thermocline causes an increase in the depth of the maximum phytoplankton accumulation. For example, at stations 25 and 26, at the edge of the Sargasso Sea, the thermocline is at a depth of 100–150 m. At these stations an accumulation of living phytoplankton was observed at depths of 100–120 m. It must be pointed out that in the last region the photosynthesis may run to some degree even at this depth because of the great transparency of water. Nevertheless the concentration of phytoplankton in the deeper water is many times more than that in the layer of optimum illumination. When entering the Sargasso Sea the thermocline disappears from the euphotic zone, and the irregular distribution of phytoplankton also disappears.

Discussion

The accumulation of living phytoplankton in the upper zone of the thermocline may not only be due to it sinking more slowly in the denser water. It may be caused by the more intensive multiplication of the algae cells in this layer because it is more rich in nutrients than those above. According to the "Meteor" data the vertical distribution of phosphate in the euphotic zone is similar to the vertical distribution of density. The thermocline zone might be supplied by nutrients from the deep cold waters by turbulence. Besides, this zone may also be supplied by nutrients by the mineralization of detritus particles and dead organisms which accumulate at the thermocline.

Our data lead to the conclusion that a relation between the vertical distribution of the living phytoplankton and the intensity of submarine illumination is observed only in the absence of thermal-density stratification in the euphotic zone. When such stratification is present the relation disappears. Thus the thermal-density stratification is one of the main factors determining the vertical distribution of the phytoplankton.

A similar relation can be assumed with regard to the thickness of the productive layer and the actual rate of production at different depths, because these are directly related to the vertical distribution of living algae. During our work in the Atlantic we have indeed observed the dependence of the thickness of the productive layer on the thermal-density stratification in the euphotic zone. Figure 5 shows typical results of parallel determinations of the thickness of the productive layer K_s; the dependence of photosynthesis rate on submarine illumination K_t; and the vertical distribution of density σ_t and temperature at stations situated in different hydrographical conditions. As we can see, in the absence of any significant stratification (stations 3a, 32, 39), the curve characterizing the thickness of productive layer, K_s, is nearly similar to that, K_t, characterizing the dependence of photosynthesis rate on light. Indeed, in this case the distribution of phytoplankton as well as the rate of its photosynthesis depends on the only one main factor—light. On the contrary, in conditions of stratification (stations 14, 23, 28) these two curves have no similarity because one of the two main factors which determine the thickness of productive layer—the distribution of phytoplankton, depends on the position of the thermocline. And we have constantly observed an increase in the actual rate of photosynthesis in the region of the thermocline.

These results show that samples for primary production work must be taken with some reference to the hydrographical conditions. It is necessary to determine the temperature stratification and in accordance with the results to choose the most suitable depths for sampling. Taking a few samples from standard depths (Jitts and Rotchi, 1958) or from a depth corresponding to definite degree of submarine illumination (as has been done by Steemann Nielsen, 1952; Steemann Nielsen and Aabye Jensen, 1957) can lead to errors because of the possibility of missing the depths of maximum accumulation of the phytoplankton. As it has been shown before, phytoplankton often accumulates in a very thin layer which may be missed quite easily.

Our results are of interest in connexion with the influence that thermal stratification and stability of the water masses have on the range of primary production and on the intensity of phytoplankton development. As it had been pointed out by some authors (Sverdrup, 1953; Hasle, 1956; Koblentz-Mishke,

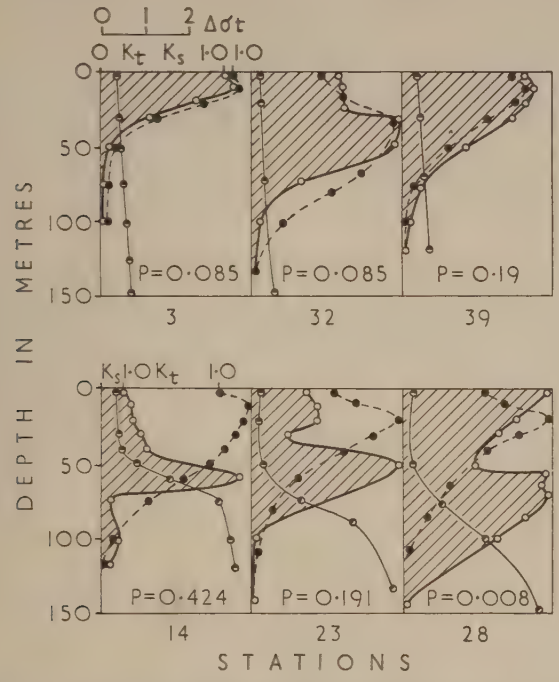

Figure 5. The vertical distribution of the rate of primary production, K_s, and the dependence of the rate of photosynthesis on light, K_t, as influenced by density stratification (δ_t).
——○—— = K_s
- - - -●- - - - = K_t
——◒—— = δ_t
P gives the primary organic production in C g/m²/24 hours.

1957). this factor is of great importance in regulating the intensity of development of phytoplankton. In conditions of instability algal cells stay for too short a period in the euphotic zone. It has been supposed that the single algae cells sink quickly into the deeper and poorly illuminated layers in the absence of the thermocline. In the presence of a thermocline they stay in the euphotic zone much longer. But on the other hand, instable water masses are better supplied by nutrients from deeper layer by convection (KETCHUM, 1947). Our data (for instance, Figures 3, 4, 5) show that absolute values of the primary production in most part do not depend on the stability of the water masses. They mainly depend upon the origin of the surface water masses and on the conditions of its supply by nutrient salts. For example, we observed the highest values of primary production at the near-shore station 1, situated in instable waters, and at the near-shore station 12, situated in very stable waters. In the open ocean we found low production even in stable waters (stations 7, 22, 23, 26) and in instable waters (stations 2a, 3a, 3, 32, 33, 39). In "young" surface waters of the open ocean we observed average values of production in stable (stations 13, 14) and in instable (station 46) conditions.

It may be supposed, that stratification of the euphotic zone which takes place *periodically* in the temperate and cold oceanic waters is a very strong factor for stimulating an intensive blooming of phytoplankton in definite seasons. On the other hand, *constantly* existing stratification in tropical waters is the main cause of the poor development of planktonic algae and their low productivity.

It is necessary to carry out more thorough investigations of this problem using radioactive isotope techniques.

Summary

1. The dependence of the vertical distribution of the living phytoplankton on thermal-density stratification was investigated in the Atlantic by the ^{14}C method.

2. It was found that in the absence of stratification the vertical distribution of phytoplankton is more or less homogenous and depends to some extent on submarine illumination.

3. In the presence of stratification in the euphotic zone phytoplankton tends to accumulate in the upper part of the thermocline.

4. Thus the rate of primary production at different depths depends not only on the submarine illumination but also on thermal stratification. Before samples are taken for primary production work it is necessary to measure the thermal stratification and to determine the position of thermocline.

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Observations on the Nile Bloom of Phytoplankton in the Mediterranean

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1. Introduction

The annual contribution of the Nile to the Mediterranean Sea from the mouths of both Rosetta and Damietta is estimated at about 34 milliard m^3 of fresh water (Ministry of Public Works, Cairo). The fertilizing effect of this periodical inflow of nutrient rich waters into an otherwise poor sea is analogous to that of the Nile on the desert lands it runs through. STEUER (1935) was first to report the exceptionally dense phytoplankton crop which follows the discharge of flood water in the neighbourhood of Alexandria. A similar "Nile bloom" occurs at Port Said (GHAZZAWI, 1939) and along the whole Nile Delta. There is evidence that the Nile flood affects the economy of the whole south-eastern part of the Eastern Mediterranean Sea up to Beyrouth (LIEBMANN,1935; ROUCH, 1940). West of Rosetta however, it does not extend beyond Alexandria. The present work is concerned only with the Damietta mouth and the area extending off Cape Ras-el-Bar. The observations were carried out during the weeks preceding and following the annual flood in 1956, 1957, and 1959 (see Figures 1 and 2).

2. Previous Investigations in Egyptian Mediterranean Waters

The cycle of zooplankton in Alexandria waters has been studied by STEUER (1935) on the basis of volume measurements of net catches. Quantitative phyto- and zooplankton investigations for the same area, together with data on salinity, temperature, and nutrients can be found in MAGHRABY and HALIM (1959). The northernmost station of GHAZZAWI (1939) in the Suez Canal provides information about the phytoplankton of Port Said for a complete year, based on net samples. Stations 4685 to 4687 of the "Atlantis" worked in front of the Nile Delta, include hydrographic observations and data on nutrients. They are

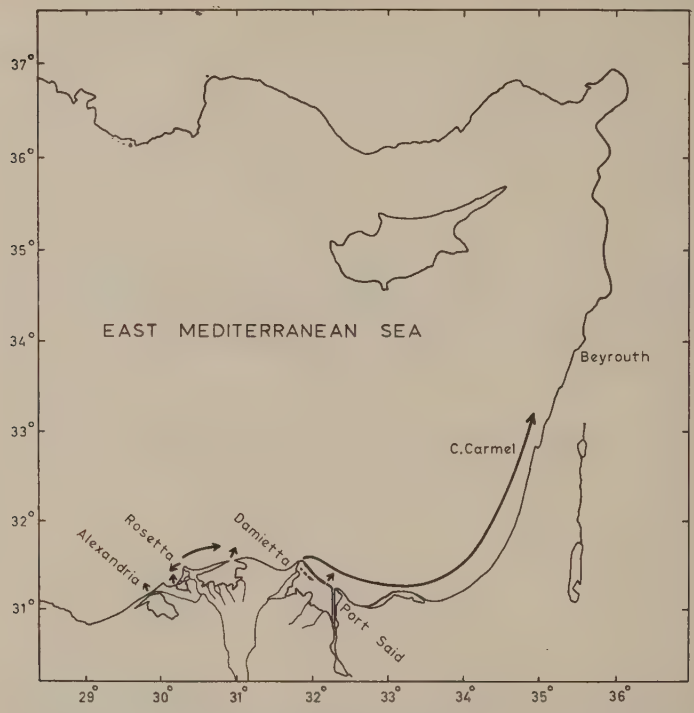

Figure 1. Chart of the East Mediterranean Sea. The arrows show the spread of the Nile waters.

published in the *Bulletin Hydrographique* (1952). The Swedish Deep-Sea Expedition has also occupied several stations in front of Rosetta and Port Said (stations 261 to 272). They include observations about the particle content in addition to hydrographic data for all, and phosphate for some of the stations.

The area of the Damietta mouth has, however, not been investigated before.

3. Methods

Salinity was determined by KNUDSEN's method. Phosphate and silicate were determined respectively after HARVEY (1948) and ARMSTRONG (1950), with small modifications in the procedure. An absorptiometer of the Spekker type was used. Nile and flood stream samples were too concentrated to be analysed as such and had to be diluted in the proportion of 1 to 10. The presence of clay and other suspended particles seems to reduce the amount of nutrients by adsorption of the ions, giving apparent concentrations which are too low. Samples analysed after removal of much of the suspended matter by filtration

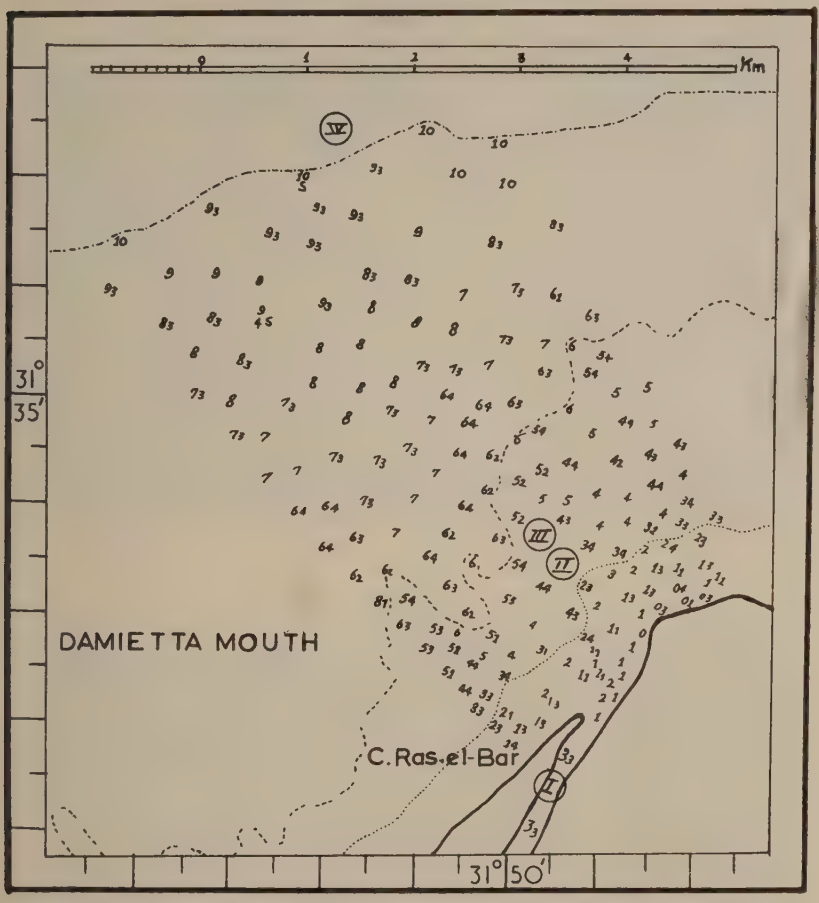

Figure 2. The Damietta mouth. I to IV, approximate position of the stations in Figure 4 and Table 4. (Soundings after Admiralty Chart No. 3567; soundings in fathoms; under eleven in fathoms and feet.)

gave 5 times less phosphate than obtained after dilution only. It is desirable to find the best conditions for a complete recovery of the adsorbed ions in turbid Nile water and work is now undertaken in this aim.

Quantitative plankton observations were obtained by the sedimentation method. About 650 ml of sea water were treated with filtered formalin and later, the supernatant water siphoned out. The sediment was transferred into calibrated tall beakers and made to exactly 200 ml. From this 1 ml, corresponding to 3·25 ml of sea water, was pipetted out after stirring and counted under an inverted microscope. All samples were taken aboard fishing boats. The positions of the stations given in Figure 2 are approximate.

4. Results

The Nile stream in the Mediterranean

A dam built 20 km up river from the Damietta mouth controls the outflow of Nile water into the sea. This dam is open only from the second week of August to the end of November. From December to the following month of August, the lower 20 km of the river are filled with sea water mixed with small amounts of brackish water from minor tributaries (Table 1). At the opening of the dam, the sea water is swept out by flood water, and a sudden drop in salinity takes place in a few hours (Table 2).

The outflowing Nile waters spread over the sea water as a thin surface layer and progress rapidly along the east coast. They reach Port Said one week after the opening of the dam, but need about five weeks to reach Palestine (LIEBMANN, 1936).

The flood stream is about 15 km in width and has sharp boundaries. Its waters are very turbid and nearly opaque; they have a characteristic reddish-brown colour, recalling that of "red" water. Only limited mixing takes place at the beginning in both horizontal and vertical directions. Photographs of the boundary between the sea and the Nile water are shown in Figure 3. At the boundary between flood and sea water, the change in salinity is very abrupt: salinity passes without transition from 12·7–17·0 ‰ to 24·4–35·4 ‰ (Table 3).

Table 1

Surface salinity at Cape Ras-el-Bar before the annual flood

Date	Salinity, ‰	Date	Salinity, ‰
4. Aug. 1956	35·32	17. Aug. 1957	33·84
9. Aug. 1956	35·01	18. Aug. 1957	33·68
12. Aug. 1956	35·52	19. Aug. 1957	33·66
		6. Feb. 1958	35·78

Table 2

Surface salinity at Cape Ras-el-Bar from 19. to 21. August, 1957

Date	Time	Salinity, ‰
19. Aug.....	1100	33·66
19. Aug.....	1900	6·94
20. Aug.....	1100	0·25
21. Aug.....	0830	0·08

Table 3

Surface salinity on both sides of the stream boundary

Stations*)..... Date	II S ‰	III S ‰	IV S ‰
August 1956	17·03	35·43	35·46
August 1957	13·75	29·43	35·41
August 1959	12·76	32·38	34·78

*) Station II: stream water, 2–3 km from the estuary, few metres from the boundary. Station III: sea water, few metres from the stream. Station IV: sea water, 5 km from the stream (except for October, 1959, 10 km).

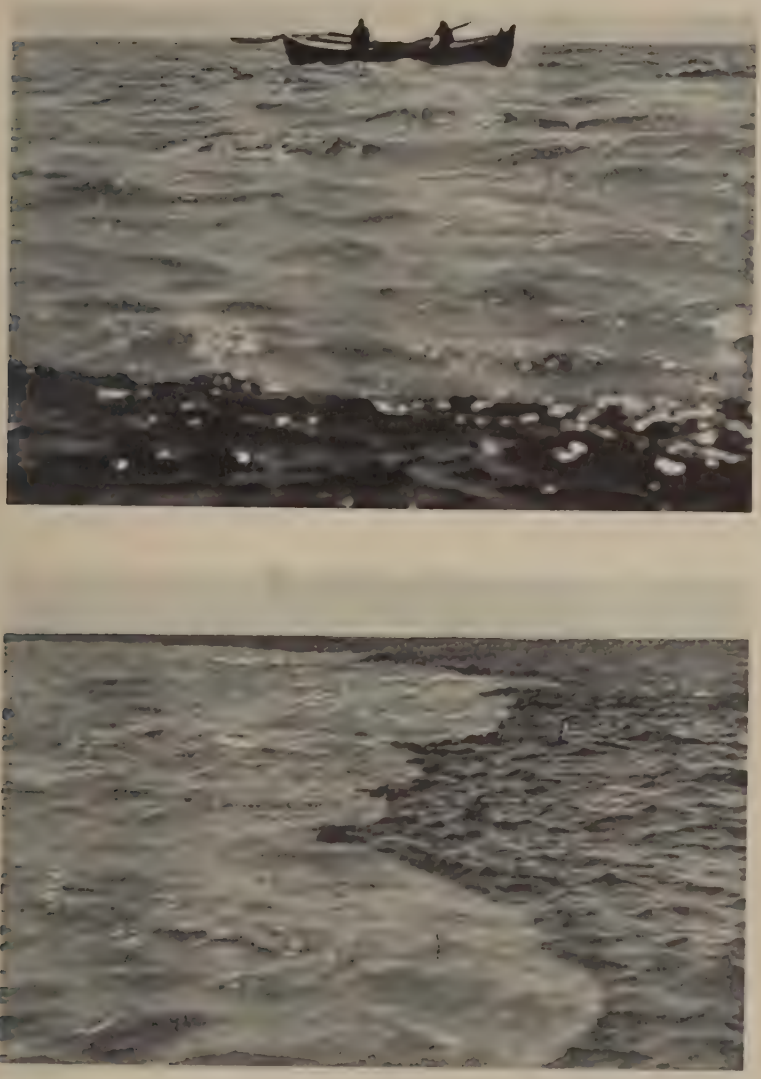

Figure 3 Top photograph taken 3-4 km off Cape Ras-el-Bar, showing the extent of the Nile stream and the sharpness of the boundary. Foreground: sea water. Bottom photograph showing the boundary between the Nile stream (to the left) and the sea water. (Both photographs by author.)

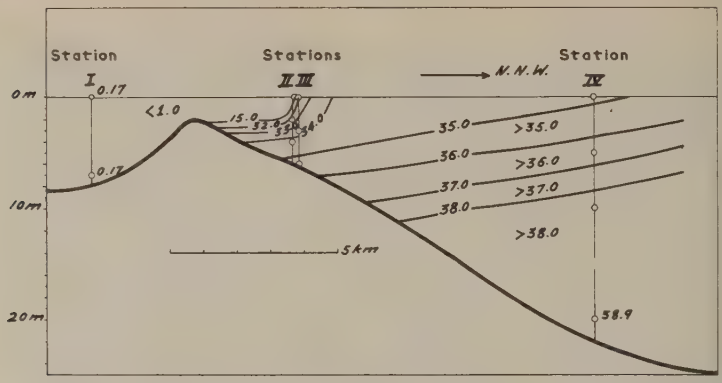

Figure 4. Section showing the distribution of salinity off Cape Ras-el-Bar, eight weeks after the opening of the Damietta dam.

The section shown in Figure 4 was taken eight weeks after the opening of the dam in 1959, from the estuary to a position about 12 km off shore. It runs in a NNW direction, i.e., at right angles to the direction of the flood stream. Unmixed Mediterranean water of salinity 38·8 $^0/_{00}$ is only found at the farthest station, below 10 m. Stations II and III, 200 m apart, are on either side of the stream boundary. The difference in their respective surface salinities is very considerable as already mentioned. The vertical change in salinity at station II is also very abrupt. A thin layer of mixed stream water (12·7 $^0/_{00}$) spreads on top of the mixed sea water (32·4 to 35·5 $^0/_{00}$). As can be seen from Table 4 the gradient is exceedingly high and the isohalines are tightly packed in the upper 2 m. The masses of fresh water continuously discharged through the estuary run eastwards along the coast between stations I and II.

Phosphates and silicates

Enormous amounts of nutritive salts are brought to the sea every year by the flood and become distributed over a wide area by the flood stream. The importance of this contribution can be seen from Tables 5 and 6. Nile water sampled 3 km up river contains up to 340·6 μg-at Si/l and 6·38 μg-at P/l. Assuming the total annual discharge from both mouths to be about 30 milliard tons, the amount of Si and P brought to the sea in this way is of 286,100 tons and 5,800 tons respectively, in four months. But the real values are probably even higher (see Section 3, Methods). Much organic matter in different forms is also carried down to the sea.

The transport of nutritive salts takes place from the stream to the surrounding waters through mixing, and very high concentrations were observed for Si 10 km from the stream (Table 6). In the vicinity of the current, in the zone where the phytoplankton bloom starts in August, the nutrients are exhausted at times or nearly so (station III, Table 5). On comparing both series of observations, although taken in different years, it can be seen that the concentration of nutrients is much lower in October than in August. This difference can be attributed to the heavy phytoplankton crop which has been produced in the preceding two months.

Table 4

The distribution of salinity at the Damietta mouth eight weeks after the annual flood

(14. October, 1959)

Station I		Station II		Station III		Station IV	
m	S ‰	m	S ‰	m	S ‰	m	S ‰
1	0·17	1	12·76	1	32·38	1	34·78
		2	32·47	3	33·87	5	36·51
7	0·17	4	34·51	6	35·43	10	38·89
						20	38·96

Port Said the same day: 29·61 ‰.

Stations: I, Nile, 3 km up river, total depth 8 m; II, stream, 3 km from the estuary, depth 6 m; III, 3·2 km from the estuary, depth 7 m; IV, 12 km from the estuary, depth 22 m.

Table 5

Surface phosphates and silicates at the Damietta mouth after the annual flood

(21. August, 1957)

	Stations*)			
	I	II	III	IV
µg-at/litre				
Phosphate	6·38	1·50	0·20	2·09
Silicate	322·5	–	0·0	60·5

*) Station I, Nile, 3 km up river; the remainder as for Table 3.

Table 6

Phosphates and silicates, in µg-at/l at the Damietta mouth after the annual flood

(14. October, 1959)

Station I			Station II			Station III			Station IV		
m	Si	P	m	Si	P	m	Si	P	m	Si	P
1	340·6	2·56	1	220·1	1·10	1	35·36	0·38	1	36·4	0·38
			2	–	–	3	–	0·38	5	–	0·38
7	–	4·27	4	–	0·35				10	–	–
									20	–	0·30

Feb., 1958; St. I, P: 0·27; Si: 9·25. For positions, see Table 4.

The Nile bloom

The quantitative observations listed in Tables 7 and 8 show the effect of the Nile flood on Mediterranean phytoplankton. Although flood waters on microscopic examination showed to contain no plankton, their discharge in the sea is immediately followed by a massive outburst of diatoms. An exceedingly dense phytoplankton crop is produced in the waters surrounding the stream. The thickness of the crop is such that the sea becomes opaque and acquires a greenish-brown colour. A slimy phytoplankton scum having a characteristic smell clogs the nets after two or three minutes.

The observations of Table 7 allow one to compare the standing crop immediately before and immediately after the flood at Cape Ras-el-Bar. The mean value for the period preceding 15. August is of 66,000 cells/litre; four days after the

Table 7

The effect of the flood on phytoplankton at the Damietta mouth in 1956 (surface)

Before the flood		After the flood	
Date	Cells/litre	Date	Cells/litre
4. Aug.	40,000	19. Aug.	1,240,000
9. Aug.	124,000	11. Sept.	2,400,000
12. Aug.	35,000		

Table 8

The quantitative distribution of phytoplankton at the Damietta mouth

(14. Oct., 1959)

Station III		Station IV	
Depth, m	Cells/litre	Depth, m	Cells/litre
1	2,347,000	1	107,700
3	1,314,000	10	70,000
7	730,000	20	70,000

Table 9

The maximum phytoplankton production in different parts of the Mediterranean Sea (cells/litre)

Locality	Cells/litre	Source
Damietta (1956)	2,400,000	–
Damietta (1959)	2,347,000	–
Algeria	759,000	BERNARD (1958)
Monaco	109,000	BERNARD (1958)
Crete	461,000	BERNARD (1958)
Split	463,574	ERCEGOVIC (1936)
Villefranche sur mer	10,000	HALIM (1956)

Table 10

A. Composition (%) of the phytoplankton in the week preceding the flood of 1956

(Station I; 4., 9., and 12. August)

	4. Aug.	9. Aug.	12. Aug.
Diatoms	81	89·1	43·0
Dinoflagellates	7·5	5·7	13·7
Ebriidae	4	5·1	43·3
Silicoflagellates	2	0	0

B. The dominant species

	4. Aug.	9. Aug.	12. Aug.
Nitzschia delicatissima	27	22	12
Leptocylindricus danicus	11	32	4·0
Hermesinum adriaticum	4	4·5	42·2
Chaetoceros affinis	8	4	14·8
Cerataulina bergoni	–	14·5	3·4
Chaetoceros decipiens	14	–	–
Biddulphia rhombus	12	–	–
Exuviella cordata	–	–	3·4
Total number of cells/litre	40,000	124,000	35,000

Table 11

A. Composition (%) of the bloom in the three weeks following the flood of 1956

(Station IV, 19. Aug. and 11. Sept.)

	19. August	11. September
Diatoms	99·9	98·5
Dinoflagellates Coccolithophoridae Ebriidae Silicoflagellates	0·1	1·5

B. The dominant species

	19. August	11. September
Skeletonema costatum	45·2	0·2
Cerataulina bergoni	0·5	55·7
Chaetoceros curvisetus	22·0	20·0
Hemiaulus sinensis	1·5	16·6
Chaetoceros costatus	14·8	0·0
Chaetoceros affinis	4·2	0·0
Chaetoceros decipiens	2·5	0·0
Rhizosolenia hebetata semispina	1·0	2·2
Leptocylindricus danicus	0·0	2·2
Exuviella cordata	0·0	1·3
Total number of cells/litre	1,240,000	1,572,000

Table 12

A. Composition of the bloom on 14. October 1959

Diatoms	99·8
Dinoflagellates	0·2
Ebriidae	0·0
Silicoflagellates	0·0
Coccolithophoridae	0·0

B. The dominant species

(Station III)

Chaetoceros socialis	96·6
Chaetoceros curvisetus	1·2
Skeletonema costatum	1·1
Hemiaulus sinensis	0·4
Nitzschia closterium	0·1
Alexandrium minutum	0·1
Total number of cells/litre	2,347,000

opening of the dam the quantity of phytoplankton reaches 1,240,000 cells/litre, and three weeks later it is even higher and reaches 2,400,000 cells/litre.

The magnitude of the standing crop in the area affected by the flood stream is exceptionally high for the Mediterranean Sea. It can be seen from Table 9 that it is more than 3 times greater than the highest values recorded up till now (at Algeria).

Composition of the bloom

Tables 11 and 12 above give the composition of the bloom and the relative abundance of the most important species. The results obtained for the week preceding the flood of 1956 are given in Table 10 for comparison. A striking fact is the presence in abundance of *Hermesinum adriaticum*, from the

rare group of Ebriidae. Although this group is known from the Black Sea, it has not been reported yet from the Mediterranean proper. The Ebriidae made up about 43% of the microplankton on 12. August with 15,000 cells/litre.

The phytoplankton population before the flood is varied in composition and although diatoms play an important role, the dinoflagellates and the Ebriidae form a significant proportion of the population. The Nile bloom is nearly exclusively due to diatoms, with the exception of *Exuviella cordata*. The Ebriidae, silicoflagellates, and Coccolithophoridae are insignificant or absent.

On 19. August 1956, the leading species is *Skeletonema costatum* followed by *Chaetoceros curvisetus* and *C. costatum*. Three weeks later, *Cerataulina bergoni* becomes dominant, followed by *Chaetoceros curvisetus* and *Hemiaulus sinensis* about equally abundant.

On 14. October 1959, the bulk of the crop is due to *Chatoceros socialis*. The same species was responsible for the bloom observed at Alexandria in September 1957 (MAGHRABY and HALIM, 1959). It is planned to follow the succession of species and their quantitative fluctuations during the blooming period at shorter intervals.

5. Résumé

1. Les présentes observations, effectuées dans les semaines qui précèdent et suivent l'arrivée des eaux de la crue du Nil à l'embouchure de Damiette en 1956, 1957 et 1958 permettent de préciser l'influence de ces eaux sur l'économie de la mer Méditerranée. Le Nil en crue débite chaque année environ 34 milliards de m^3 d'eaux douces. Les eaux déversées s'étalent en surface (Tableau 4) formant un courant nettement délimité (Tableau 3 et figures), large de plus de 15 km et dirigé vers l'est. L'influence de ce courant se fait sentir jusqu'au large du Cap Carmel (Paléstine) et même de Beyrouth.

2. Les eaux de la crue apportent chaque année à la mer de grandes quantités de sels nutritifs et de débris organiques divers (environ 286·100 tonnes de Si et 5·780 tonnes de P; voir Tableaux 5 et 6). Cet apport périodique provoque instantanément une pullulation massive des diatomées au mois août de chaque année (Tableaux 7 et 8). Le stock biologique passe en quelques jours de 66.000 à 2.400.000 cellules par litre d'eau. La région traversée par le courant du Nil représente ainsi la région la plus productive de la Méditerranée (Tableau 4).

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Evidence of Cod (*Gadus morhua* L.) Migrations from the Norway Coast to the Faroese Islands

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During routine examination of otoliths from cod caught by the F.R.S. "Explorer" off the Faroe Islands two pairs of otoliths were found that had a structural pattern differing considerably from that typical of Faroese cod but strongly resembling that of Arcto-Norwegian cod. In particular the nuclei of the atypical otoliths were fairly uniform in structure without pronounced splits. The second and third opaque zones showed some splits. These were fewer and less pronounced than those of Faroese cod otoliths in which these splits make it difficult to distinguish the winter hyaline zones with certainty (Plate 1).

The fish from which these otoliths were taken were considerably larger than any other specimens sampled for age determination, being 121 cm and 118 cm total length compared with a maximum of 109 cm among fish with typical Faroe otoliths. Growth curves calculated from the two pairs of otoliths and from typical Faroese and Arcto-Norwegian otoliths show that the two atypical fish have a growth-rate similar to that of Arcto-Norwegian cod (Fig. 1). A linear relationship between fish length and otolith growth has been assumed.

It is therefore considered that these two atypical cod were derived from the Arcto-Norwegian stock. There is no record of a tagged cod from the Arcto-Norwegian stock being caught at the Faroe Islands, despite the large number of fish tagged and the intensive fishing off the Faroes, which suggests that there is no substantial movement between the two areas.

Long distance movements of cod between different sea areas are well known, fish tagged at Iceland having been recaptured off the Norwegian coast (JÓNSSON, 1953) and off the Faroes (TÅNING, 1937), and cod tagged off Bear Island from the R.V. "Ernest Holt" being caught off Greenland and off Iceland (unpublished data).

There are two possible ways in which these movements could occur. Either there is an orientated movement directly between the two areas, for the most part against the prevailing currents, or there is an unorientated drift in the anti-clockwise current gyral in the Greenland Sea.

A direct movement from the Norwegian coast to the Faroes would entail the fish swimming across water deeper than 1000 fathoms, and in order to orientate themselves it would be necessary for the fish to swim in contact with or in sight of the bottom unless there is orientation to the sun. Cod have been

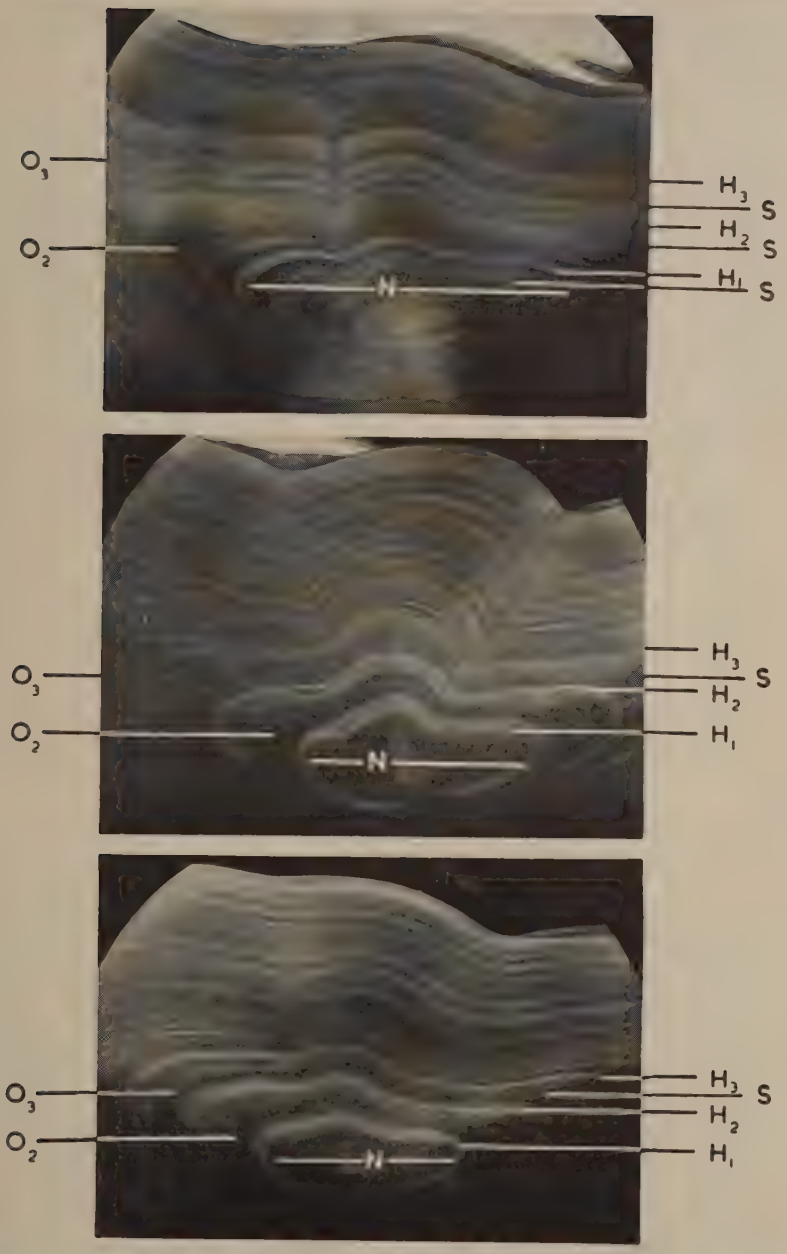

Plate I. Typical Faroese (top) and Arcto-Norwegian (bottom) cod otoliths with atypical cod otolith (centre). (N = nucleus, O = opaque zone, H = hyaline zone, S = splits; suffixes denote years.)

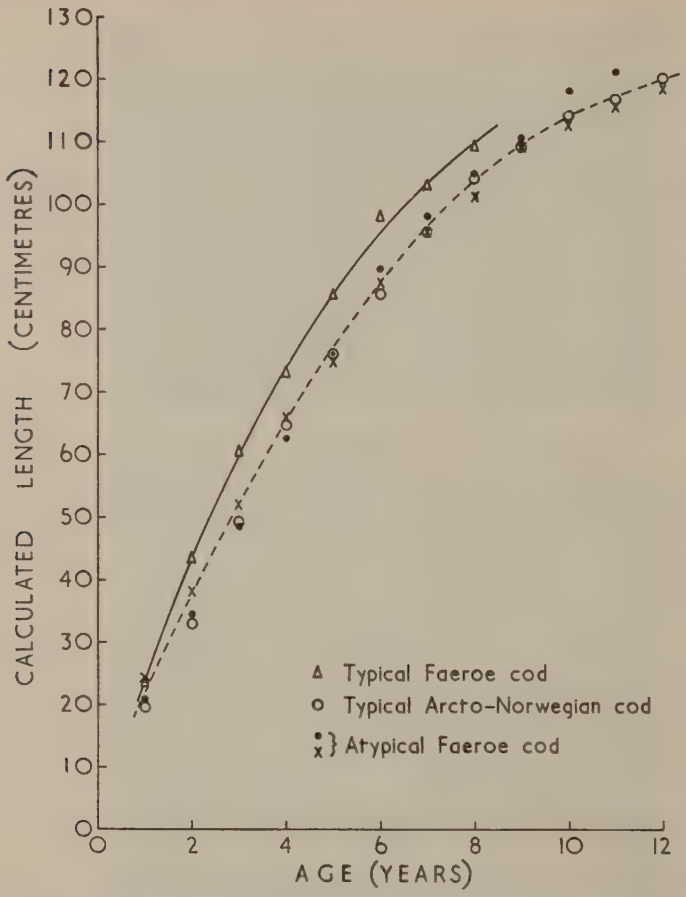

Figure 1. Growth-rates calculated from otoliths (linear relationship assumed). Rates for typical Faroese and Arcto-Norwegian cod taken from the otoliths illustrated in Plate 1.

caught in this area, but only on long-lines and not in a trawl (JENSEN, 1905), indicating that they are swimming not demersally but pelagically, in which state they would be unable to orientate themselves to the current and would drift with it. There is considerable evidence that such movements are a passive drift in the currents. TÅNING (1937) quotes four cases in which the time taken for cod to move between two areas closely approximated to that taken by drift bottles.

The main current in the Greenland Sea is the Atlantic Current, which flows from the Faroe-Shetland Channel along the Norwegian coast. This gives rise to the West Spitsbergen Current, an offshoot of which turns west from Spitsbergen to eventually flow under the East Greenland Current, some of which

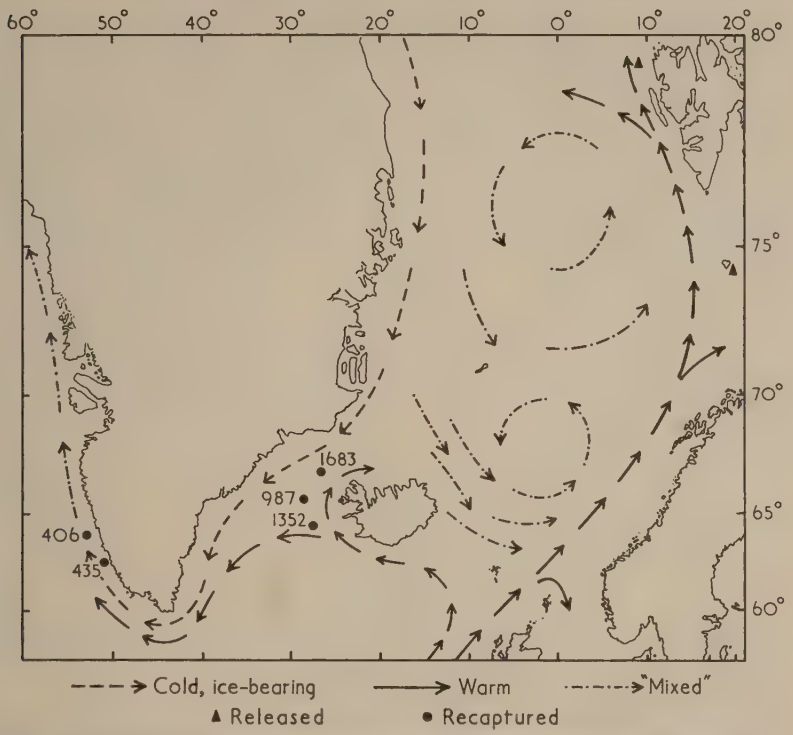

Figure 2. Greenland Sea, showing main currents and positions of recapture of tagged cod, together with number of days at liberty.

turns south-east to join the East Icelandic Current, the remainder flowing round Cape Farewell to form part of the West Greenland Current. Between the West Spitsbergen, East Greenland, and East Icelandic Currents are a series of eddies of "mixed" water (Fig. 2.).

Returns from tagging carried out from the R.V. "Ernest Holt" show that there is some movement of cod from Bear Island and West Spitsbergen to Greenland and Iceland. The number of days at liberty, 406 and 435 days for two recaptures off West Greenland and 987, 1,352, and 1,683 for three recaptures between East Greenland and north-west Iceland indicates that this movement is first to West Greenland, in the East Greenland Current, and then to Iceland, against the Irminger Current. The lack of returns outside this area suggests that these cod remain with the Icelandic-Greenland stock and do not migrate further to reach the Faroes.

Therefore fish that reach the Faroes must either leave the East Greenland Current or remain in the eddies of "mixed" water, in either case eventually joining the East Icelandic Current. The lack of recaptures of cod tagged from the Arcto-Norwegian stock at the Faroes and their presence at Greenland suggests that fish joining the East Greenland Current are always carried by it

to Greenland and that fish reaching the Faroes do so in the eddies between the main current systems, the final migratory path only being in the East Icelandic Current. Cod tagged at Jan Mayen have been recaptured off Iceland (IVERSEN, 1934), and JENSEN (1905) fishing in the Greenland Sea trawled up several gadoid otoliths, including one cod otolith. These were found most frequently at the stations between Jan Mayen, north-east Iceland, and the Faroes, and were assumed to have come from pelagically swimming cod that had died and which would have been swimming in the East Icelandic Current. DEVOLD (1952) suggests that part, at least, of the Atlanto-Scandian herring stock follows this route.

Summary

1. Two pairs of otoliths from cod caught at the Faroes were found to have a structure similar to that of Arcto-Norwegian cod otoliths and dissimilar to that of Faroese cod otoliths. It is concluded that the fish originated from the Arcto-Norwegian stock.

2. The path of movement between the two regions is discussed. It is shown that it most probably lies in the anti-clockwise current gyral in the Greenland Sea and that there is a drift with the currents from Spitsbergen via Jan Mayen and north-east Iceland to the Faroes.

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Preliminary Results of Tagging Experiments with Herring (*Clupea harengus* L.) in Greenland

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Introduction

The herring, *Clupea harengus* L., occurs in Greenland waters along both the west and the east coast, but in small quantities only. Its distribution is shown in Figure 1. It is most commonly found in the Julianehaab district, but is also frequently met with in large numbers in certain localities in the Frederikshaab and Sukkertoppen districts.

Otto FABRICIUS mentions the herring in his "Fauna groenlandica" published in 1780, but at that time it was hardly as numerous as today, even though at Frederikshaab it was a well-known fish, which was now and then captured by the Greenlanders. During the present warm period the stock of herring has probably increased in number, but the fishery to which it is subjected is of minimal importance, and the tagging experiments likewise show that it is hardly present in particularly great numbers. Up to about 1950 a small herring fishery was carried out in the Julianehaab district, where the herring was bought from the Greenlanders to be salted at the sheep-breeding station. In recent years the catch has hardly been larger, but the herring is now only used for consumption, and to a very modest extent it is frozen and used as bait on the cod long-lines.

It is only during the summer that the herring is observed and captured along the coasts of Greenland. It appears in early summer in bays and coves in shallow water, where the spawning likewise takes place close to the coast line in August-September. Where the herring spends the winter, is not known with certainty, as its presence has never been ascertained by means of the echo-sounder in the fjords or along the shore, nor has it been found in the stomach contents of cod. In the winters of 1957–58 and 1958–59, however, herrings were captured by means of jigs in quite shallow water off Tasiussak in Tasermiut Fjord (Nanortalik district). The Greenlanders' normal summer fishing for herring takes place with set gill-nets or hand seines.

According to investigations by HANSEN the herring caught at West Greenland show racial characters identical with the summer spawning herring of Iceland

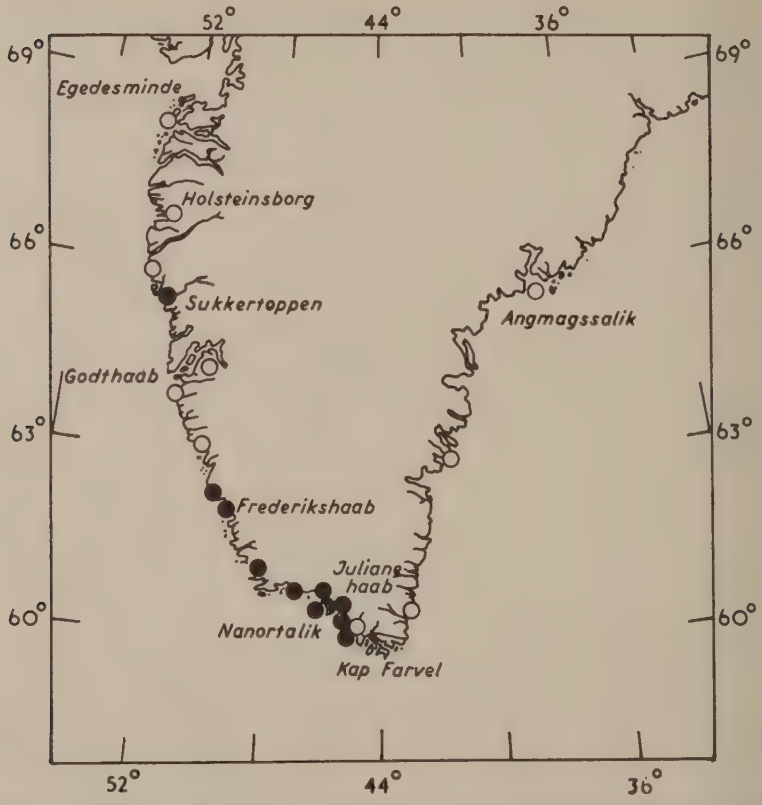

Figure 1. Distribution of herring in Greenland. Closed circles indicate localities where fishing is regularly carried on. Open circles indicate scattered occurrences.

Table 1

Number of vertebrae of Greenland herring

Locality	North latitude	Year	Number of vertebrae	Number of specimens
Sukkertoppen	65°30′	1930	57·10	101
Avigait	62°15′	1932	56·89	172
Sardlok	60°35′	1932	56·94	150[1])
Sardlok	60°35′	1930 and 1932	56·92	100

[1]) Spawning herring.

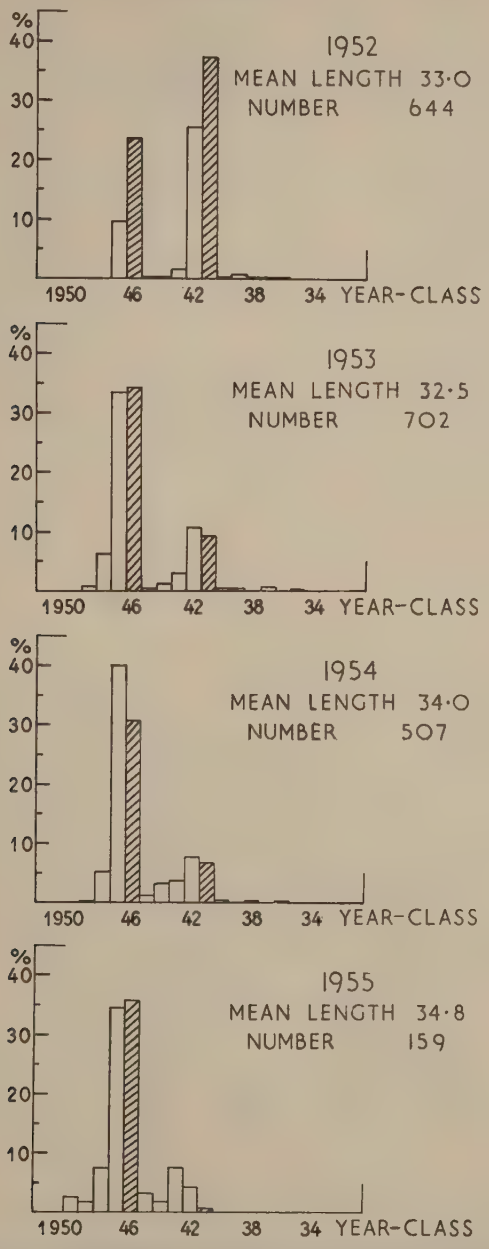

Figure 2. Age composition of Greenland herring from the Julianehaab district 1952–1955. The mean length indicated is total length in centimetres.

Table 2

Growth of Greenland herring. Mean total length in cm of the dominating year-classes in 1950–1956

Year	Year-classes 1947	1946	1942	1941
1950	14·0	19·9	–	–
1951	–	–	–	–
1952	26·9	30·4	36·1	37·1
1953	29·7	31·7	36·2	37·2
1954	31·9	33·2	38·2	39·2
1955	34·0	35·3	–	–
1956	34·9	36·2	–	–

(TÅNING, 1936). HANSEN concludes there probably is only this one herring race in Greenland (HANSEN, 1934). Table 1 shows the number of vertebrae from different samples of Greenland herring.

Age determinations have been undertaken by HANSEN and NIELSEN. Some preliminary results have been published (HANSEN, 1937, 1939, and 1940; NIELSEN, 1955, 1956, and 1957). A special publication on the age investigations on Greenland herring is prepared by the author. Figure 2 shows the age determinations of a few samples from Julianehaab district. It is evident that certain year-classes are dominating in the catches. The growth of the herring is shown in Table 2, where the mean lengths of the dominating year-classes are given in different years.

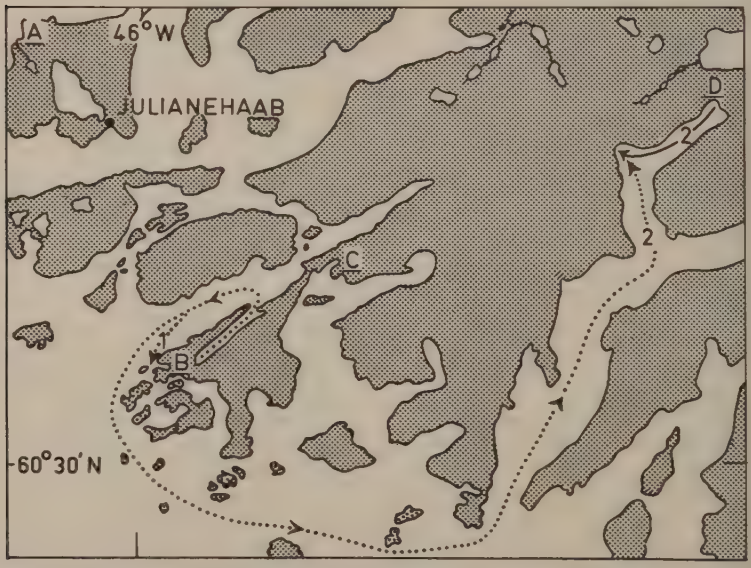

Figure 3. Migrations of the herring in the Julianehaab district. The letters indicate the tagging localities (see Table 3). The figures at the dotted lines indicate the number of tagged herrings migrated from the place of tagging to the localities of recapture.

Tagging Methods

In the years 1949 and 1952–54, tagging of a small number of herrings, totalling 451, was carried out by the Greenland Fisheries Investigations. A later tagging experiment, started in 1958, is of such a recent date that it will not be mentioned here.

The tagging localities of the experiments in 1949 and 1952–54, with the exception of the locality of Kangerdluarssuk in the Sukkertoppen district, are shown in Figure 3. Table 3 is a survey of the taggings and the recaptures made so far. Further recaptures from these experiments can hardly be expected.

All the herrings tagged were captured near the shore by means of hand seines, which are dragged to the shore. In 1949 Lea hydrostatic tags were used for tagging, while later on plastic tags attached by black terylene spinner line (breaking strength 11 lbs.), were employed. In the experiments in 1958 the tags were fastened by soft stainless wire, diameter 0·40 mm. The tags were attached to the front edge of the dorsal fin. In 1949 and 1952 the herring was measured when tagged, but in subsequent experiments the herring was not measured, for in such case the fish can be kept under water during the whole tagging process. While under water, the herring is driven into a small rubber case of the shape of a shoe, and by this procedure touching of the fish by the hands may be almost avoided.

Results

Hitherto no recaptures have been reported from the taggings in 1949 and 1952. Whether this is due to the somewhat more rough tagging method employed in these two years, when the herring was taken out of the water and measured, can hardly be decided on the basis of such a small material. In 1953, 100 herrings were tagged at Sukkertoppen, 31 of which were recaptured three weeks later in the same place. No later recaptures have been reported from this tagging experiment, but the recaptures made shortly after showed, however, that the herring was capable of surviving the tagging, and the tagging experiments were therefore continued in 1954.

In 1954, three tagging experiments were made, two at Sangmissoq (B in Fig. 3), and the third at Amitsuarssuk at the head of Lichtenau Fjord (D in Fig. 3). From the tagging experiments at Sangmissoq, when altogether 158 herrings were tagged, two were recaptured the next day in the same place. One was recaptured at Kangerdlugssuagtiaq, located 17 km from the place of tagging. Two had migrated to Qagdlimiut in Lichtenau Fjord (see Fig. 3), a distance of about 75 km. This indicates that the herrings from the different fishing grounds are intermixed, so it is not exclusively the same herring that return every summer to the same locality.

At Amitsuarssuk in Lichtenau Fjord (D in Fig. 3), 88 herrings were tagged. Eight of these were recaptured next year, six of them in the place of tagging, while two were taken at Qagdlimiut, which is located farther out in the same fjord hardly 10 km from the tagging place (see Fig. 3).

If in the experiment at Sangmissoq we disregard the two herrings recaptured the next day, twenty-one of the 244 herrings tagged in 1954 were recaptured the next year, which means a recapture percentage of 8·6. It must be taken for granted that a great many herrings will die as a result of the taggings, the herring

Table 3

Tagging experiments with herring in Greenland and recaptures

Tagging					Recapture				
Year	Date	Locality	Type of tag	Number	Date	Locality	Number	Number of months in the sea	Distance migration in km
1949	8. Aug.	A. Eqalugarsiut, Jhb.	Lea hydrostatic	15	–	–	–	–	–
1952	21. Aug.	B. Sangmissoq, Jhb.	Yellow plastic	65	–	–	–	–	–
1952	25. Aug.	C. Itivdliatsiaq, Jhb.	Yellow plastic	25	–	–	–	–	–
1953	11. June	Kangerdluarssuk, Skt.	Yellow plastic	100	June 1953	Same place	7	0	0
					July 1953	Same place	24	1	0
1954	9. Aug.	B. Sangmissoq, Jhb.	Red plastic	83	Aug. 1954	Same place	2	0	0
					June 1955	Same place	2	10	0
					June 1955	Kangerdlugsuagtiaq	1	10	17
					July 1955	Qagdlimiut	2	11	75
					July 1955	Same place	3	11	0
1954	16. Aug.	D. Amitsuarssuk, Jhb.	Red plastic	88	July 1955	Qagdlimiut	2	11	10
					July 1955	Same place	6	11	0
1954	18. Aug.	B. Sangmissoq, Jhb.	Red plastic	75	June 1955	Same place	3	10	0
					July 1955	Same place	2	11	0
			Total	451		Total	54		

being a very delicate fish and difficult to tag, so this recapture percentage is fairly high—more especially if it is taken into consideration that the herring fishing within the district is not particularly intensive, but is carried out quite casually and occasionally by a few Greenland fishermen.

The relatively high recapture percentage suggests that the herring population in Greenland is rather small. The tagging experiments likewise show that it is the same herring which return to the herring grounds summer after summer, though migrations take place between the various fishing grounds. This was also to be expected, for by investigations of the age of the Greenland herring it has turned out as already mentioned that it is special year-classes which are dominant in the catches. The recaptured herrings from the taggings at Amitsuarssuk, where very big herrings were tagged (32–42 cm total length), were 12–14 years old. The recaptured herrings from the other two taggings were 7–9 years old, a single one, however, being 12 years old.

As regards nine of the recaptures, the questions on the recapture label as to whether the fish was sound or ill when recaptured, are answered. Five of these were stated to be sound (and mature), while four were stated to be ill (and immature). This may perhaps indicate that the tagging process or the tag itself may be injurious to the herring.

Summary

Herring occur in small numbers in the coastal waters of Greenland, particularly in southern West Greenland, where a small herring fishery takes place in summer when the herring migrate to the inner parts of the fjords to spawn. In the years of 1949 and 1952–54 tagging experiments were made. The recaptures show that the herring for the most part return to the same fjords summer after summer, though sparse migrations may take place from individual localities to others. The comparatively high recapture percentage shows, considering the low intensity of the herring fishery that the herring are present in small numbers only.

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Progress in Observing Tuna Underwater at Sea

By

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1. Introduction

The world's increasing demand for protein food makes it imperative that we improve the efficiency of harvest for those resources whose crops are not easily manipulated. In the central Pacific such a resource is oceanic skipjack, *Katsuwonus pelamis* (L.), a small surface-schooling tuna which is one of the most valuable seafoods in the area. Studies of larval skipjack (MATSUMOTO, 1958) and adults (IKEHARA, 1953; MURPHY and IKEHARA, 1955; WILSON and AUSTIN, 1959) indicate the species to be widespread and locally abundant, but in spite of this it is not exploited to the extent warranted by world demand. One factor limiting its capture is bait fish (TESTER, 1951; YAMASHITA, 1958), for most skipjack are caught by live-bait methods, and the bait species are usually delicate and in short supply. In the central Pacific these conditions restrict the fishery to waters adjacent to baiting grounds, and for these and other reasons the resource in large portions of the open ocean is untouched (SCHAEFER and REVELLE, 1959). A promising approach to the problems of increasing fishing efficiency, developing baitless techniques of capture, and exploiting new bait species is the understanding of skipjack behaviour as it is related to the fishing method. This subject, especially the equipment developed during our studies of it, forms the basis for the present report.

To obtain data on behaviour it was first necessary to devise a method of making underwater observations. A study of captive skipjack seemed to be precluded by earlier failures to maintain these fish in ponds and tanks (TESTER, 1952), and, in addition, it was desired to study their behaviour under fishing conditions. Placing an observer or a recording device beneath the surface from a fishing vessel was a logical solution to the problem.

2. Method of Fishing for Skipjack

An account of the present Hawaiian skipjack fishery has been given by JUNE (1951). Suffice it to say that commercial fishing is done from the sterns of 60–80 ft motor vessels from which skipjack schools are located by means of

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Figure 1. Tuna fishing from the port side and stern of the "Charles H. Gilbert." Small yellowfin tuna are being caught here, but the same technique is used for skipjack.

the accompanying bird flocks. The birds and tuna prey in common on small fish and squid, and, in order to engage the tuna, live-bait chum is used to divert them from their natural food. During fishing, sprays of water are directed into the sea around the stern where, according to the fishermen, they enhance the effects of the bait.

The HBL research vessel "Charles H. Gilbert", a 112 ft steel-hulled ship, was designed for a variety of research tasks including skipjack fishing. A view of the port side of this ship, looking aft, is given in Figure 1; four men occupy the two side fishing racks, while the pole of a fifth man is visible in the third (stern) rack. Above them, and partly obscured by pipework, is the "chummer" whose station is on top of a large baitwell, whence he throws live baitfish into the water near the fishermen's lures. The rack framework is composed of pipes carrying water for use as spray; a spraying nozzle is visible near the second fisherman's knee. Because of such factors as chum abundance, wake and stream flow effects, and possibly propeller noise, there is a gradient in fishing activity. Action is greatest beneath the closest fisherman in Figure 1 and least at the stern. For behaviour study purposes attention was focused on activity beneath the two side racks.

3. Evaluation of Observation Equipment

Ladder and diver

Our first attempt to place an observer underwater took place in June 1957. Because of the exploratory nature of the study, equipment was inexpensive and simple: A diver made observations from a 10 ft steel ladder on the ship's port side.

Figure 2. Diver descending overside ladder of "Charles H. Gilbert."

As shown in Figure 2, the diver was equipped with a face mask, mouthpiece, regulator, and hose leading to a bottled air supply on deck, a weighted belt, and protective diving clothing. He descended the ladder and crouched on its lower rungs, facing aft. Depending on his stance, his eyes were 1–2 ft beneath the surface. He carried a 16 mm Cine camera in a waterproof case, and between dives made voice records of his impressions. There was no provision for communication except a system of knocks on the ship's hull or ladder. The ladder itself was a 2 in. steel pipe with welded rungs of $\frac{1}{2}$ in. steel bars. Three brackets held it to the ship while in use, and at other times it was pivoted out of the water as shown in Figure 3.

The diver-ladder technique was used only in bays, but it provided answers to several questions. It told us that a diver could be effectively positioned beneath the ship, and that bubbles from propeller cavitation were not a serious hindrance to his vision. Its cheapness and simplicity made this method a qualified success; its defects are listed below.

The method's principal disadvantages involved the diver's safety, utility, and comfort. The ship had to be slowed or stopped in order for him to ascend or descend the ladder, and once he was in place, speeds greater than about 3 knots tended to tear the mask from his face. The current, the ship's roll, and

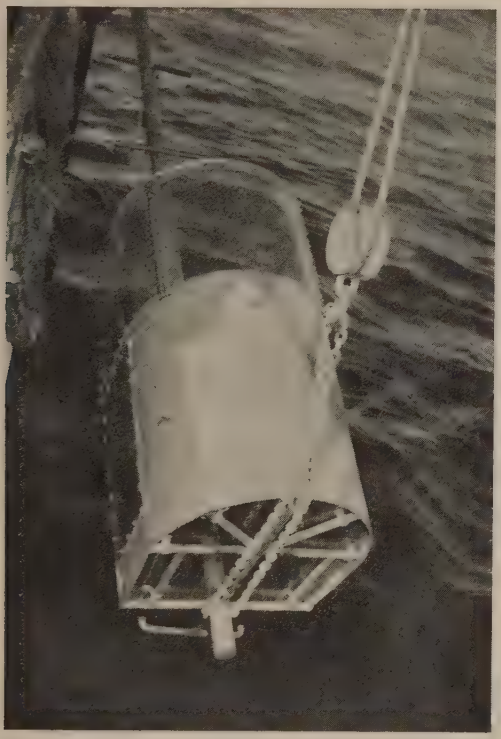


Figure 3. Shield used to protect diver on overside ladder.

ladder vibrations were sometimes sufficient to require his using both hands to remain on the ladder, thus prohibiting picture taking. The current rapidly chilled him, in spite of protective woolen and rubber clothing, and it also caused sore jaws from biting the regulator mouthpiece against the current's drag. Bubbles exhaled by the diver or dragged down around the ladder from the surface tended to obscure vision. There was an important time loss when he ascended to replace the film in his encased camera or to record his observations. Last, but certainly not least, was the psychological effect of being completely exposed during fishing in waters where sharks are common.

A solution to some of these problems was offered by partially enclosing the diver in a 4 × 2 × 2 ft U-shaped steel and plastic shield (Figures 3 and 4). Besides protecting him from the current and sharks, this provided a more comfortable place to sit. Squatting or kneeling on the transparent floor of the cage, he could photograph in response to knocks from the surface indicating a change of bait, etc. His forward and lateral vision was through windows of $\frac{1}{2}$ in. transparent plastic; facing aft, where the skipjack were concentrated, there was nothing intervening except two ladder rungs. The shielded ladder was tested several times from June to August, 1957. These tests were quite rewarding, and following them it was decided that construction of a more permanent observation platform was warranted.

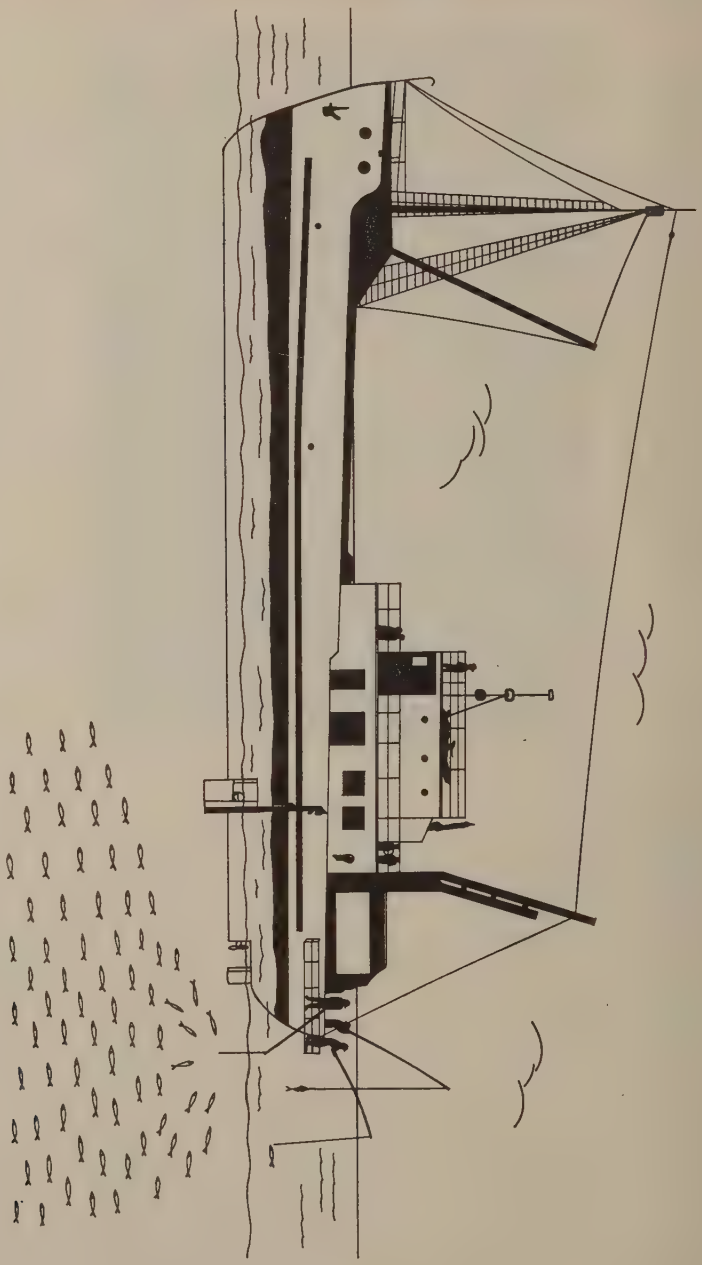


Figure 4. Position of shielded ladder and diver during skipjack fishing.

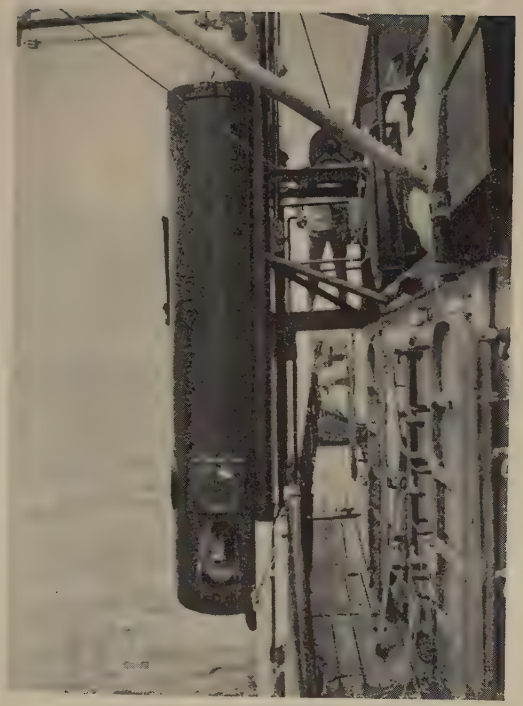


Figure 5. Observation caisson hauled from water after fishing.

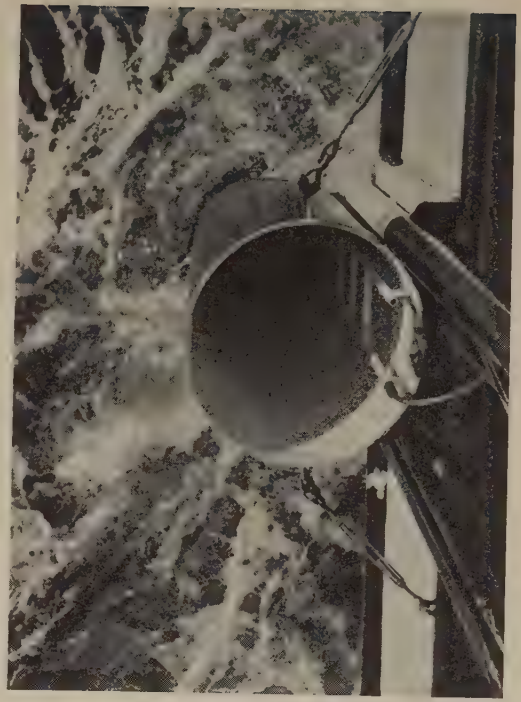


Figure 6. Caisson in its fully lowered position. Note turbulence and bubbles.

Overside caisson

Many of the unsatisfactory aspects of the 1957 apparatus were inherent in the use of a diver. During the succeeding winter, therefore, plans were made for placing an observer beneath the surface in a retractable air-filled cylinder. Such a device was built in the spring of 1958, and was extensively tested on the "Charles H. Gilbert" during May-July. Observations made from this caisson have been discussed by STRASBURG (1959) and STRASBURG and YUEN (in press), but the apparatus itself has not been described.

As originally constructed (Figure 5), the caisson was a $11\frac{1}{2}$ ft tube, open at the top, with four ports at its lower end. Just prior to fishing this tube was partially submerged by means of pulleys and a hand crank; after fishing it was raised from the water by its own buoyancy and the same pulleys attached in a different manner. The caisson was movably fixed to the ship by two 6 ft T bars which bore against the inside of extra-heavy slotted 4 in. pipes (Figure 6). A short length of pipe on the bottom of the caisson provided rigidity by fitting into a gudgeon 6 ft below the waterline. Accidental bobbing-up of the caisson was prevented by shackles, sister hooks, and turnbuckles securing it to the ship's rail in the lowered position (Figure 6).

An observer reached the viewing ports of the submerged caisson by a ladder. With his eyes 4 ft below the surface, he sat on a low stool and took moving pictures from a 5 in. forward port ($\frac{1}{2}$ in. plastic), a 12 in. side port, or two 10 in. after ports (side and after ports of $\frac{3}{4}$ in. glass). Communication with the surface was via a speaking tube leading to a recorder microphone. Fresh air was blown to the bottom of the caisson by way of one of the ladder's sidepieces (Figure 6). Water splashing over the top or leaking around the window seals accumulated beneath a false bottom, whence it could be drained by a valve or aspirated by a hose. In practise, except in all but flat calm seas, it was necessary to cover the top with a wooden hatch (not shown) to prevent flooding.

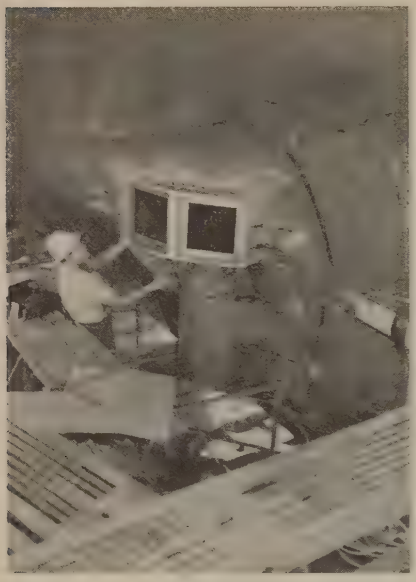
Some other statistics of the caisson are of interest in evaluating its utility. Its walls were of welded $\frac{1}{4}$ in. steel plate, and were not quite circular in cross section, being 28 × 30 inches in outside dimensions. The empty weight was about 1350 lbs. Water drag gradually misaligned the T bar bearings and their pipe guides, so that increasing amounts of time, up to 10 minutes, were required for lowering. This resulted in a costly pause, in terms of bait expenditure, while the crew hammered and tugged at the recalcitrant caisson. With the caisson lowered, the ship cruised at 7·5 knots instead of its normal 9, making it difficult to approach fast-swimming tuna schools. Even at this reduced speed bubbles blocked all vision except from the forward port. Dense clouds of bubbles were drawn down around the caisson and tended to collect in the recessed faces of the ports. At speeds of 2–3 knots (usual fishing speeds) turbidity was reduced to an occasional but annoying swirl of bubbles. Horizontal visibility was about 100–150 ft, depending on the object, but skipjack could be distinguished from other tuna species only to about 60 ft.

The caisson, as described above, was used to evaluate the effects of several fishing variables (dead bait, water sprays, various bait species, chumming rate, and sound) on skipjack feeding behaviour. Five weeks of such experiments provided ample opportunity for appraising the caisson. Turbidity provided the biggest problem, for bubbles sometimes rendered as much as 75% of the Cine camera film useless for detailed analysis. Another annoying feature was

Figure 7. The redesigned observation caisson.

salt water splashing on the observer or his equipment, even with the top of the caisson covered (heavy seas sometimes opened the cover, drenching the observer). A third unfavourable feature was the restricted vision aft, where both ports were small and one slanted downward and was seldom used. Few tuna schools were lost because of the ship's stopping to lower the caisson, but this did happen occasionally and was not desirable. The advantages of the caisson over the preceding ladder are obvious and require no discussion.

The "Charles H. Gilbert" was engaged in other duties in mid-summer, 1958, so the caisson was temporarily removed and modified. Its height was increased by adding a 4 ft section to the top (Figure 7), and portions of the slotted pipe guides were removed in an attempt to reduce bubble formation. The two after ports were replaced by a single 12 ⁄ 24 in. pane of ½ in. plastic. The hand crank for raising and lowering the caisson was removed, and power for doing this was instead supplied by the anchor winch. The improved 1600 lb caisson functioned satisfactorily during the period August–November, 1958. The added height kept out all water, and the enlarged after window gave increased latitude for picture-taking. The caisson could be lowered rapidly, often in 1½ minutes, and there was little time loss from this factor. Shortening the pipe guides had no appreciable effect on turbidity, however, and this feature continued to be the most serious drawback to the caisson's use. By November 1958, it was decided that bubble-free vision was sufficiently important to justify new observation instruments.



(a)

(b)

(c)

Figure 8. (a) Fabricating metal portions of stern blister. (b) Profile view of stern blister. Windows are at vertical upper edge of blister. (c) Side view of completed stern blister. Windows and concrete fairing have been added.

Stern blister

An obvious means of reducing bubble interference was to place a window in the ship's hull below the waterline. This was regarded as a last resort, for it meant possibly weakening the vessel, relinquishing space needed for fuel, and perhaps reducing the ship's speed and steering qualities by the drag resulting from a protuberance. Nevertheless, in June 1959, the "Charles H. Gilbert" was placed in drydock and a convex observation "blister" added to the hull in communication with a former fuel compartment. Stages in the fabrication of this installation are shown in Figure 8.

Space for the observer was provided by welding a steel semi-cylinder, 22 in. in diameter and 3½ ft high, to the ship's skin outside the former fuel tank (Figure 8a). Surmounting this cylinder was a wide sill on which the observer could rest his arms or equipment. This sill was fronted by two 12 × 12 in. windows of 1 in. glass set 7 ft below the waterline. Steel reinforcing provided anchorage for an outer concrete coating which was sprayed on in liquid form, and hardened as a 1 to 12 in. layer which streamlined the blister. The completed structure, shown in Figures 8b and c, held two people, but only one could look out conveniently. The blister's bulge was minimal, and the ship cruised at 9 knots as before. Steering at normal cruising speed required no rudder compensation, but when maneuvering slowly, as in docking, the bow tended to starboard.

Observers enter the blister through a covered vertical access-way on the after main deck. A ladder and a series of steps lead to the semi-cylinder, where they can stand or sit comfortably. They and their equipment are dry at all times, and forced draft ventilation makes the blister one of the more pleasant places aboard ship. The previous bubble-turbidity problem is entirely eliminated, and objects such as sheets of newspaper or masses of *Sargassum* can be seen near the surface up to ranges of about 200 ft. Typical skipjack activity as seen from the blister is shown in Figure 9.

The blister was employed extensively during July–September, 1959. Observation from it was so easy, and occasionally so enjoyable, that in addition to experimental tests of skipjack behaviour, data were obtained on animals attracted to submerged lights, luminescent organisms, plankton net operation, composition of windrows of phytoplankton, underwater feeding of seabirds, and animals associated with drifting logs. Observations could have been made on bottom conditions and the undersides of waves.

As constructed the blister had two faults: its proximity to the tailshaft and propeller resulted in a high noise level, and its permanently submerged windows quickly became covered with sessile marine life. Noise ceased to be an important problem when sound-powered telephone headsets were used, and window cleaning required only a few minutes of a diver's time about twice a week.

Television

Concurrently with the first blister tests, we explored the use of closed-circuit television for studying tuna behaviour. Information was desired on the utility of a television camera mounted in the blister and another suspended over the side in a waterproof case. Skipjack activity recorded by these means was compared to that seen directly by eye, and to that recorded by a Cine camera

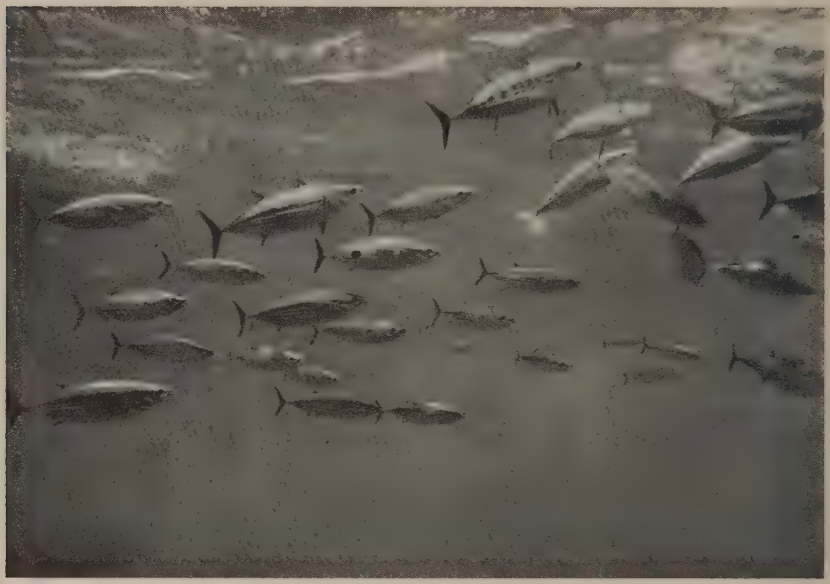


Figure 9. School of oceanic skipjack seen from the stern blister.

using colour film. Because only monochromatic television equipment was available, black-and-white Cine films were taken of the television screens.

An encased Vidicon television camera was attached to a rigid pipe framework and lowered over the side of the "Charles H. Gilbert" to the depth of the blister windows. Operations were coordinated, and fish scenes were observed, televised, and photographed simultaneously. Using 525 scan-lines per second and a 10 in. screen, the televised presentation was inferior to the eye's view. With television, fish outlines were indistinct, species could not be distinguished, contrast between fish and background was poor, portions of the screen were black, and a full-time technician was required to operate the controls. Substantially the same thing was shown by comparing the filmed versions of this, but here television appeared to have greater depth of field, and therefore more fish were visible. This virtue was offset by fluctuations in brightness and erratically moving horizontal bars, both possibly being synchronization phenomena. Television did not detect the numerous small animals swarming around a submerged light at night, but proved remarkably sensitive for observing bottom life. When the encased camera was lowered to the bottom in 92 ft of water, algae (*Padina*) and fish (*Acanthurus*) were easily identified, even during the rapidly changing light conditions preceding sunset.

Simultaneous operation of television and film cameras from within the blister was only partially successful. Apparently the ship's vibration affected the television camera, so that bright bars sporadically obliterated images on the screen. Exclusive of this, Cine camera or visual observation was still superior to the televised version.

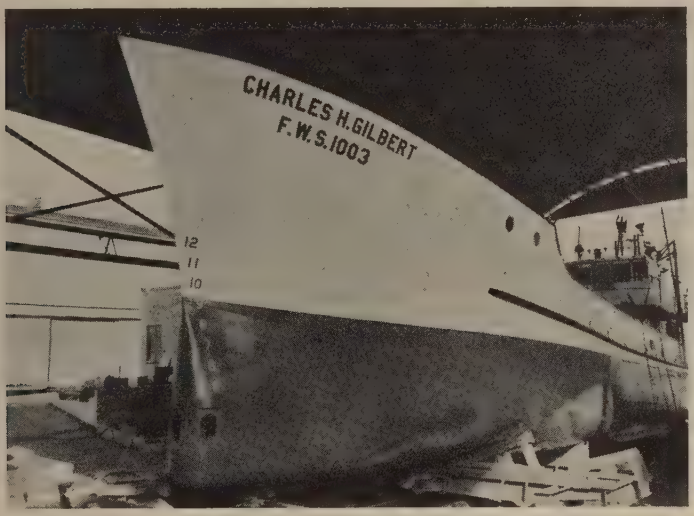


Figure 10. Construction of the bow blister on the "Charles H. Gilbert."

Bow blister

Although well adapted for observing feeding behaviour, the stern blister was too near the center of fish activity for out-lying skipjack to be seen. Thus we only suspect, and do not know, that the members of feeding aggregations are constantly leaving as they become satiated, and are constantly being replaced by hungry fish, the entire phenomenon being associated with a deep-swimming body of non-feeding fish. The physical dimensions and numbers of fish in a feeding aggregation are similarly difficult to ascertain. More information on these points could be obtained if the blister could be maneuvered around a school being fished by another ship. It is possible to do this with the stern blister but it will be much more easily accomplished with a similar structure located in the bow.

At this writing the "Charles H. Gilbert" is being fitted with the bulbous bow and observation blister shown in Figure 10. This blister is equipped with three 12 × 18 in. oval windows of 1 in. glass, behind which the observer will lie. His head will be 7 ft beneath the waterline, and his working space a long, high compartment, 3 ft wide. Access to the bow blister will be by ladder from the forecastle storage spaces, and communication is by sound-powered telephone. Ventilation is forced-draft.

4. Future Plans

An outstanding limitation of all the above approaches is that information is gained only about skipjack at or near the surface. Nothing is known of their activities at depths greater than about 100 ft, although there are indications that these activities may be significant. We have evidence (unpublished) that schools are attracted downward, in competition to our chum, by schools of

natural food such as squid. Also, several hundred hours spent searching the surface layers from the stern blister have failed to reveal any really small skipjack. Fish weighing a pound or less should be much more numerous than the adults, and it can be surmised that they occur at depths greater than we can see.

For these reasons we are presently investigating the feasibility of constructing a small, fast, highly manœuverable submarine for studying skipjack behaviour to depths of about 400 ft. As envisioned, schools of adults would be located at the surface and followed downward, and underwater searches would be made for sizes not occurring at the surface. Observations would be by eye and camera through forward ports, and by television cameras facing in other directions. Acoustical apparatus and lights would aid in locating fish beyond visual range. Additional missions might include collecting plankton and water samples under selected conditions of depth, temperature, light intensity, or salinity; studies of biological sound, etc. An obvious failing of this method would be the near-impossibility of actually capturing skipjack, but this would be offset by the wealth of other information obtained.

5. Acknowledgements

Several members and former members of the Honolulu Biological Laboratory (HBL) staff participated in the design and use of underwater observational equipment. Mr. G. I. MURPHY initiated the investigation with an underwater ladder carrying a diver. MURPHY, V. E. BROCK, and the writers subsequently developed a dry caisson, and in the following years BROCK and the writers designed hull blisters and worked with underwater television. Messrs. H. J. MANN and A. K. AKANA, by drawing plans, fabricating models, and supervising construction, were closely involved with all such equipment, and their help is gratefully acknowledged. The photographs used in Figures 2 and 3 were supplied by the Honolulu Star-Bulletin.

6. Summary

Equipment for studying tuna behaviour underwater on the high seas is described. Starting with a ladder and diver, the staff of the Honolulu Biological Laboratory has progressed to a shielded ladder, an overside caisson, stern and bow blisters, and underwater television. Future plans involve a small, fast submarine. The principal faults and virtues of each device are noted.

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Efficiency of Particle Retention and Rate of Water Transport in Undisturbed Lamellibranchs

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Introduction

The amount of food available to a suspension feeding lamellibranch is determined by the rate at which the surrounding water is transported through the gills and by the efficiency with which suspended food particles are retained. Quite naturally, therefore, many determinations have been made of the rate of water transport and the porosity of the gills in various lamellibranchs; especially in oysters and mussels. However, the results obtained by different investigators often vary or even disagree. Thus, much higher rates of water transport were measured in mussels by JØRGENSEN (1949) than by FOX, SVERDRUP and CUNNINGHAM (1937), RAO (1953), and WILLEMSEN (1952). And whereas some investigators found that particles as small as one or some few microns were almost completely retained from a suspension passing the gills in mussels and oysters (JØRGENSEN, 1949; JØRGENSEN and GOLDBERG, 1953), others obtained widely varying retention of particles even as big as 30 microns or more (LOOSANOFF and ENGLE, 1947; TAMMES and DRAL, 1955).

Some of the differences in results may express real differences in the rates of water transport and efficiency of particle retention in normal, undisturbed lamellibranchs, but the main reason for the discrepancies are probably to be sought in different experimental techniques; lamellibranchs are very sensitive towards changes in their environment and they may react on even slight stimulation by diminishing the water transport and by altering the mode of functioning of the feeding organs (MACGINITIE, 1940).

Quantitative data on feeding in lamellibranchs would clearly be of greater value if they can be shown to have been derived from experiments on undisturbed animals. Therefore, an attempt was made to determine rates of water transport and porosity of the gill filters under conditions that were hoped to be compatible with normal feeding in undisturbed animals. Water transport and porosity were determined by measuring the rates at which suspensions of particles of various sizes were cleared by the animals. The rates of clearing, in the following termed clearances, have been expressed in litres of suspension

cleared of particles in one hour. Experiments were made on the mussel *Mytilus edulis* (L.) and the scallop *Pecten latiauratus* Conrad.

Rates of water transport are generally expressed in relation to the size of the animals, such as the weight of the soft parts. Even greater interest attaches to the relationship between the rates of water transport and of oxygen consumption (see p. 113). In some experiments, therefore, rates of both water transport and of oxygen consumption were determined in the same animals.

The water transport in mussels has been found to vary with the tidal cycle (Rao, 1954). And mussels (*Mytilus californianus*) from the upper tidal zone have been found to transport water at lower rates than did mussels from the lower zone (Segal, Rao, and James 1953). The present study offered an opportunity for re-testing whether the water transport in mussels can be correlated with the tidal cycle or with the level in the tidal zone at which the mussels are sampled. No correlations appeared.

Material and Methods

The experiments were made at the Mount Desert Island Biological Laboratory, Maine, and the Scripps Institution of Oceanography, California.

In Maine, experiments were made on three groups of *Mytilus* (Table 1). The mussels in groups 1 and 2 were collected in a large tide pool from the mid-tidal zone; those in group 3 at the lower end of their vertical distribution, on rocks just below the locality from which the two other groups were obtained. The mussels of the third group were probably exposed only during extreme low water.

In California, experiments were made on a group of four *Mytilus* collected on 10. March from rocks in the tidal zone. The animals were 26 to 31 mm in length (mean 29 mm) and had a mean wet weight of 0·55 g. The experiments ended 28. March. Further experiments were made on a group of four *Pecten*, 22–27 mm in length, collected in Mission Bay, California, on the 27. March and used in experiments until 17. April. While stocks of *Mytilus* survived in apparently good health for at least several months in the running sea water of the laboratory, *Pecten* began rapidly to die off after about a month: apparently the scallops did not thrive under the experimental conditions.

The animals were kept in 1–2 l glass jars from which they were not removed during the experimental period. The jars were placed in larger aquaria in which the water level could be adjusted so that the glass jars were completely immersed

Table 1

Mytilus edulis **used in experiments at the Mount Desert Island Biological Laboratory, Maine**

Group	Number of mussels in the groups	*Length in mm* Average	Range	Average weight of soft tissues in g*)
1	11	37	27–44	1·44**)
2	12	31	26–35	0·80
3	10	32	25–38	1·09

*) The tissues were scraped from the shells and quickly dried on filter paper before the weighing.

**) Tissues dried at 106°C weighed 21 % of the wet tissues.

between the actual experiments, when the water level was kept just below the upper edge of the glass jars. Between experiments sea water circulated through the glass jars before entering the aquarium, so that the animals were supplied with ample amounts of sea water from the tanks of the laboratories. In Maine, this water contained sufficient food to produce conspicuous growth of newly metamorphosed mussels and barnacles that had been placed in the aquarium.

Before the clearance determinations or measurements of oxygen uptake were to be made, the glass jars were emptied, and faeces and other sediments that had accumulated around and between the mussels were washed away. When the running water again covered the mussels, they soon re-opened their shells and extended their siphons in a normal manner. If clearance determinations were to be made, the water level in the aquarium was adjusted so that the upper edge of the glass jar was exposed, then the glass tubing through which the water entered the jar was removed, and the suspension to be tested was added to the jar. Initial mixing of the suspension and the sea water in the jar was secured by repeatedly sucking up some of the contents of the jar into a glass syringe and blowing it out again. If carefully performed, this procedure hardly disturbed the mussels. Mixing was performed, in California, by bubbling air through the suspension, but as *Mytilus* are so easily disturbed by mechanical stimuli, aeration was not used in Maine. Instead, the size and shape of the glass jars were chosen such that the mussels, when pumping water at normal rates, kept the whole volume of water well mixed (Jørgensen, 1949). Care was taken to see that the clusters of mussels anchored close together were all freely to extend their siphons without taking each others exhalent water.

Clearances were measured by suspensions of diatoms, colloidal graphite, haemocyanin, and haemoglobin.

1) Cultures of the diatom *Asterionella japonica* which forms colonies about 200 μ in diameter were used, as these are probably too big to pass between the gill filaments. Clearances of *Asterionella* suspensions, therefore, equal the rates of water transport through the gills. The diatom was cultured in radioactive phosphorus. The concentration of diatoms in suspension was determined by measuring the radioactivity of 1 ml samples evaporated to dryness (Jørgensen and Goldberg, 1953).

2) Colloidal graphite was used to represent particles of the size of small flagellates and bacteria, that is, the smallest living organisms constituting a potential source of food to filter feeders. In most experiments the preparation Aquadag A was used, but a few experiments were also made with Prodag. (The preparations were manufactured by the Acheson Colloids Corporation, Port Huron, Michigan, U.S.A.) The dominating particle size of both Aquadag and Prodag is 1–2 μ, but Prodag contains a greater proportion of larger particles than Aquadag. Stable, concentrated suspensions were prepared by vigorously shaking the graphite in distilled water. Before the clearance determinations were made a small amount of the stock suspension in distilled water was mixed thoroughly with sea water. This dilute suspension was then ready for use.

In sea water the colloidal graphite coagulates, Prodag much faster than Aquadag. Whereas the average particle size in freshly prepared suspensions of Aquadag is still 1–2 μ, the size increased to some 2–3 μ within from one half to a few hours. In about one day all graphite is deposited as macroscopic particles (Dales, 1957; Jørgensen and Goldberg, 1953).

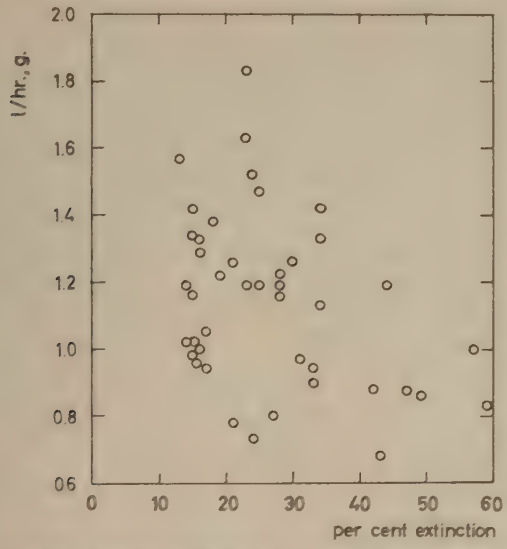

Figure 1. Relationship between clearances of colloidal graphite and initial concentration of graphite, expressed as the extinction relative to pure sea water, read on the photometer. A 10% extinction corresponds to about 2 mg graphite per litre of suspension. Clearances (in l/hr.) are expressed per g wet weight of soft parts.

The graphite concentrations were determined colorimetrically. In California a Beckman Model DU spectrophotometer was available; using 10 cm cells it was possible to use initial concentrations of graphite as low as 0·2 mg l. In Maine, measurements were made by means of a Bauch-Lomb spectrophotometer; and the initial concentration of graphite had to be at least about 2 mg l to provide sufficiently accurate determinations of clearances.

In order to see whether the high graphite concentrations influenced the filtering activity of the mussels, the effect of graphite concentration on clearances was investigated. From Figure 1 it is seen that the clearance was independent of the initial value at concentrations giving a transmission higher than about 65% of the transmission in pure sea water. At higher concentrations the clearances tended to decrease. In the following, only clearances determined in experiments with initial graphite concentrations giving more than 65% transmission have been considered. A 90% transmission was found to correspond to some 2 mg graphite per litre. In most of the experiments, the initial concentration was 2–3 mg l. Such concentrations are not excessively high, as often they did not induce any pseudofaeces production, even when the animals were filtering at normal rates. As the graphite was efficiently retained by the gills (see p. 100), the mussels were thus capable of ingesting all the material that could maximally be gained in suspensions initially containing 2–3 or even more mg l. The extensive ingestion of the material collected by the gills indicates that the mussels were undisturbed by the experimental conditions (Mac Ginitie, 1941).

3) Haemocyanin was obtained from the American lobster, *Homarus americanus*. The haemocyanin was stained with Evans Blue, T 1824, by diluting lobster blood 1:10 with sea water containing 100 μeq T 1824 per litre. The diluted blood was filtered through a glass filter in order to remove blood cells and clots. The filtered solution was diluted 1:4 with pure sea water before being used in the experiments. In order to see how much of the dye was adsorbed on the haemocyanin which is practically the only protein present in the serum of lobster blood, the haemocyanin was precipitated in a sample by saturation with $(NH_4)_2SO_4$. The precipitate was a strong blue colour, and no significant amounts of T 1824 could be demonstrated in solution. The initial concentration of haemocyanin in the experiments corresponded to a dilution of lobster blood of 1:2000. If the protein concentration in the blood is assumed to be about 4% (Eliassen, 1953), the suspension contained some 20 mg protein per litre. Changes in haemocyanin concentrations were measured by means of the Bauch-Lomb spectrophotometer. Readings were made at 6100 Å. When clearances of haemocyanin and graphite were determined simultaneously, readings were made both at 6100 and 5000 Å. At 5000 Å the extinction was due practically only to the presence of graphite, and its removal from the suspension could therefore be followed separately.

4) Haemoglobin was obtained in solution by haemolysing, in distilled water, the red cells from centrifuged blood of the dogfish *Acanthias squalus*. After filtration and dilution with sea water, the haemoglobin solution was added to the mussels in such small quantities that no measureable light absorption due to haemoglobin was found when readings were made at 5000 Å, but about 8% extinction when readings were made at 4100 Å, at which wave length maximal extinction was measured. The measurements were made on the Bauch-Lomb photometer.

The clearances in the various suspensions were calculated as follows. The concentrations of the suspensions, as read on the photometer during an experiment, were plotted on semi-logarithmic paper as a function of the time. The straight line judged to fit the plots most closely was drawn, and the clearance was calculated from the rate of decrease in concentration indicated by the slope of this line. In fitting the line, most weight was given the points representing the first readings in an experiment, because the higher initial concentrations could be more accurately determined.

By far the greater number of clearance determinations were made with suspensions of colloidal graphite. An attempt was made to estimate the accuracy of the determinations by connecting the point representing the initial concentration with those later points that represented the fastest and slowest removal of graphite respectively. Some randomly chosen examples are shown in Figure 2. The maximal and minimal clearances calculated on basis of the slope of such pairs of lines differed on an average by 20%, and seldom by more than 40%.

Oxygen was estimated according to Winkler. When oxygen consumptions were to be measured, the running water to the glass jar containing the experimental animals was stopped, and a close-fitting glass lid placed on top after an initial sample of water had been siphoned off. The oxygen content of the water did not fall below 3·7 ml per litre during any experiment. At this concentration the oxygen consumption is not significantly lower than in water saturated with atmospheric oxygen (Gaarder and Eliassen, 1954; van Dam, 1954).

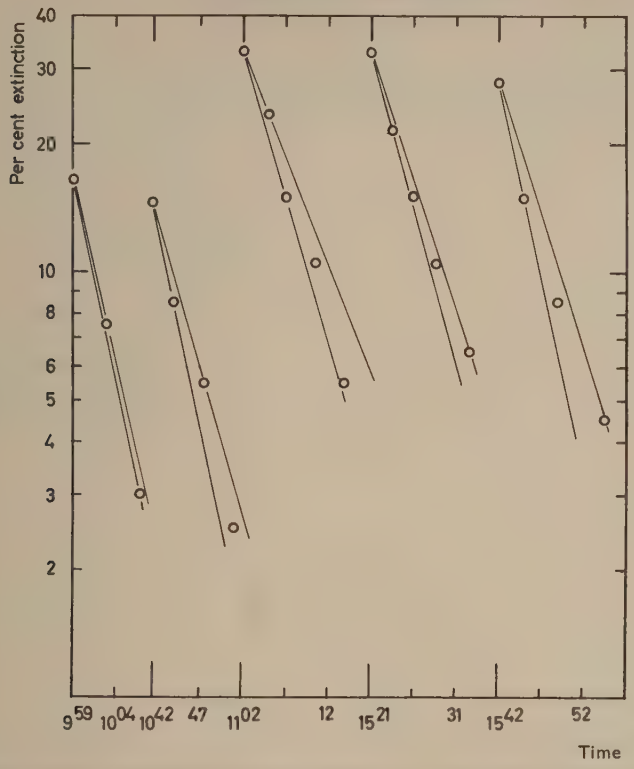

Figure 2. Rates of removal of colloidal graphite by *M. edulis*. The experiments were made on one day at the times shown on the abscissa. Ordinate: concentrations in logarithmic scale. Further explanation in the text.

The water in the jars was not stirred mechanically, but was of course circulated by the animals. In a control experiment with *Mytilus*, water samples were siphoned from various levels in the jar at the end of the experiment. The oxygen in the water fell from an initial value of 5·63 ml/l to 3·70 ml/l in the upper part of the jar, 3·86 ml/l in the middle, and 3·94 ml/l in the lower part, demonstrating that the whole volume was well circulated during the 17 hr. duration of the experiment.

No correction was made for oxygen consumption due to bacterial activity during the experiments, because it was assumed that the experimental animals kept the number of bacteria in the water so low that their oxygen consumption was negligible. This assumption is probably justified in the case of *Mytilus* which efficiently retain particles of bacterial size, but is more doubtful in the case of *Pecten* (p. 106). Control experiments showed that in the absence of the experimental animals, filtered water consumed about 0·01 ml oxygen per hour during a period of 17 hours; in unfiltered water the consumption was five times as high. In the presence of the *Mytilus* or *Pecten* a total of 0·2 to 0·6 ml oxygen were consumed per hour.

Table 2

Clearances of *Mytilus edulis* in suspensions of colloidal graphite (Aquadag A)

Experiments made at the Mount Desert Island Biological Laboratory, Maine.

Clearances in l/hr./g wet weight of soft tissues

Group	Date	Locality	Temp. °C	Age of graphite suspensions in hours: < ½ Average	Range	Number of determinations
1	11.–14. July	Mid-tidal zone	13	1·07	0·73–1·42	12
2	24. July–2. Aug..	Mid-tidal zone	14			
3	6.–9. Aug.....	Lowest end of tidal zone	14	1·69	1·48–1·91	3

Group	Date	Locality	Temp. °C	Age of graphite suspensions in hours: ½ — 6 Average	Range	Number of determinations
1	11.–14. July	Mid-tidal zone	13	1·25	0·68–1·83	24
2	24. July–2. Aug..	Mid-tidal zone	14			
3	6.–9. Aug.....	Lowest end of tidal zone	14	1·61	0·76–2·13	11

Group	Date	Locality	Temp. °C	Age of graphite suspensions in hours: > 18 Average	Range	Number of determinations	Group Average
1	11.–14. July	Mid-tidal zone	13	–	–	–	1·19
2	24. July–2. Aug..	Mid-tidal zone	14				1·65
3	6.–9. Aug.....	Lowest end of tidal zone	14	1·58	1·15–2·01	5	1·59

Average of all determinations: 1·48

Results

Mytilus edulis

Porosity of gill filters

Retention of colloidal graphite. The rates at which *Mytilus* (from Maine), cleared graphite from the suspensions are collated in Table 2. The results are arranged according to the age of the suspensions. It is seen that the clearances were at most slightly lower in suspensions less than half an hour old than in suspensions ½ – 6 hours, or more than 18 hours old. As the average particle size in old suspensions is many times larger than in fresh suspensions, it follows that either the gills were impermeable to all sizes of graphite particles down to about 1 μ, or a constant fraction of particles were retained, independent of their size, during each passage through the gill filters. The first possibility is of course the most likely and is further strongly supported by the finding that clearances similar to those obtained in the Maine experiments were also obtained in the California experiments, where *Mytilus* did in fact efficiently retain graphite particles of one to a few microns in size (JØRGENSEN and GOLDBERG, 1953). Presumably, therefore, the gill filters of *Mytilus* retained efficiently even 1 μ graphite particles, the dominating particle size in fresh suspensions.

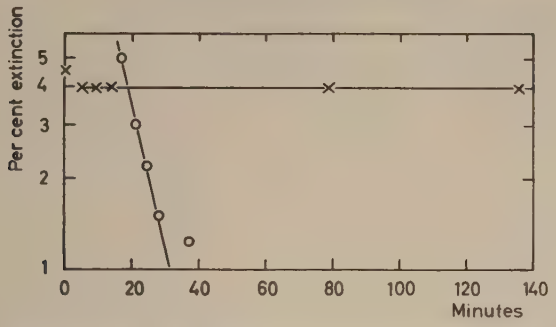

Figure 3. Rates of removal by *M. edulis* of lobster haemocyanin (×) and colloidal graphite (○) simultaneously present in suspension. Concentrations, i. e. extinctions, of haemocyanin were read at 6100 Å; and of graphite at 5000 Å. Freshly prepared graphite suspension was used.

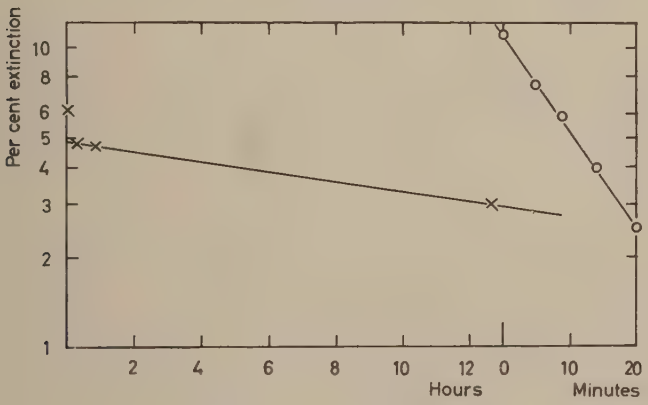

Figure 4. See text to Figure 3. One day old suspension of graphite used.

Retention of haemocyanin. In Figures 3 and 4 are shown typical examples of the rate at which lobster haemocyanin was removed from suspension as compared with the rate of removal of graphite. It may be seen that the clearances of haemocyanin were so low that accurate determinations were not possible; and in the example shown in Figure 3 the haemocyanin concentration did not fall measurably in two hours, even when the freshly prepared suspension of graphite was cleared at a rate of 1·2 litre/hr./g. The average rate of water transport by the mussels in pure graphite suspensions was 1·65 litre/hr./g (Table 2, group 2). It is obvious, therefore, that the presence of the haemocyanin did not significantly influence the porosity of the gills towards graphite, or the rate at which water was transported through them.

The experiment shown in Figure 4 lasted 12 hours. At the end of this period the mussels were less open than normally, and graphite when added was cleared at a lower than normal rate, viz. 0·72 l/hr./g. The average clearance of haemocya-

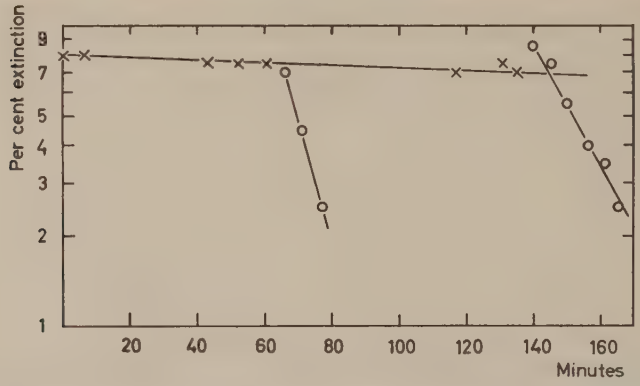

Figure 5. Rates of removal by *M. edulis* of dogfish haemoglobin (×) and colloidal graphite (○) simultaneously present in suspension. Extinctions of haemoglobin were read at 4100 Å; and of graphite at 5000 Å.

nin over the 12 hour period was 0·007 l/hr./g. The mussels, therefore, at most retained about 1% of the haemocyanin passing the gills under conditions where 1 μ graphite particles were retained almost completely.

The stock suspensions of haemocyanin were found to agglutinate slowly. The rapid initial fall in haemocyanin concentration which was regularly seen in the experiments (see Figs. 3 and 4) was most probably due to a relatively efficient retention of the agglutinated fraction of the added haemocyanin.

Retention of haemoglobin. Similarly, the rates of removal of dogfish haemoglobin by *Mytilus* were so low that the degree of retention could not be accurately determined. In the experiment shown in Figure 5, the clearance of haemoglobin was about 0·01 litre/hr./g, whereas graphite added one hour after the addition of the haemoglobin was cleared at the normal rate of 1·44 litre/hr./g. The graphite suspension was 2 hours old, so that the average particle size was probably not higher than about 2–3 μ. The haemoglobin, therefore, did not reduce the rate of water transport or increase the porosity of the gills; but the haemoglobin molecules were nevertheless retained to less than 1%.

Rate of water transport

It has been seen from the results discussed above that the rates at which suspensions of colloidal graphite were cleared by *Mytilus edulis* equalled the rates at which water was transported through the gills. From Table 2 it is seen that the average rate of water transport, in the experiments made in Maine was 1·5 l per hour and gramme wet weight of the soft tissues, at 13–14°C.

In the experiments made in California both rates of water transport and oxygen uptake were measured on the same animals (Figure 6). The average rate of water transport, 1·4 l/hr./g, was similar to that obtained in Maine. Oxygen was consumed at an average rate of 0·095 ml/hr./g. About 14·5 l of water were thus filtered for each ml of oxygen taken up.

The values of the clearances of graphite varied from 0·68 to 2·13 l/hr./g (Table 2), or much more than can be due to inaccuracies in the method of

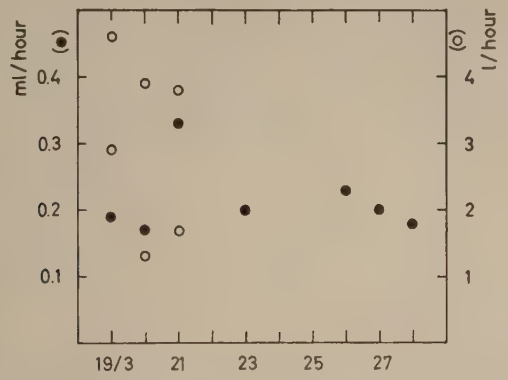

Figure 6. Rates of water transport (○) and oxygen consumption (●) in four specimens of *M. edulis*. Total wet weight of soft parts 2·2 g. Temp. 14–17°C. Abscissa: dates of experiments. The mussels were brought into the laboratory 10. March.

determination (see p. 98). The variations, therefore, most probably reflect variations in the rates at which the mussels were transporting water in the various experiments. Two factors that might be thought responsible for at least some of the variations are considered presently; other factors will be discussed later.

Tidal cycle and rate of water transport in *Mytilus edulis*

In *Mytilus californianus* and *M. edulis*, Rao (1954) observed that the rate of water transport varied synchronously with the tidal cycles: high tides coincided with maxima in water transport, as determined by clearances of colloidal graphite, and low tides with minima. The tidal rhythm persisted for several weeks in the laboratory.

The relations between clearances of graphite and the tidal phases in the present experiments are shown in Figures 7 and 8. In Figure 7 are plotted all clearances determined in Maine on the mussels of groups 1, 2, and 3, in relation to the time intervals between the determinations and the nearest high or low tide. Figure 8 shows all determinations of clearances made on group 1 in the course of one day, the only day on which several clearance determinations were made both at the high and the low tide. It is apparent from the figures that the rates of water transport did not vary with the tidal cycle. Thus, the tidal rhythm in filtering activity that the mussels—at least in groups 1 and 2—most probably exhibited in their natural environment was lost in the laboratory. The large variation in the rate of water transport which could be observed even in experiments performed on the same day with the same group of mussels (Figure 8) must, therefore, be due to some other factor.

It is not clear why tidal variation was observed in Rao's but not in the present experiments on *M. edulis*. The mussels used by Rao were obtained from Woods Hole, Massachusetts (the experiments were performed in Los Angeles, California), and there is no obvious reason why tidal variation should be shown by mussels from Massachusetts, but not from Maine. However, the experiments

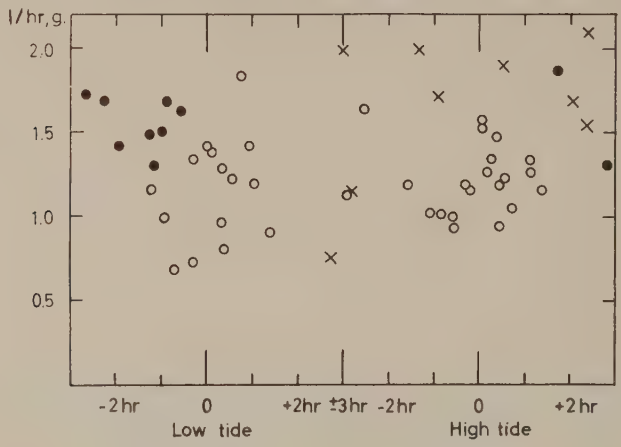

Figure 7. Relationship between water transport in *M. edulis* and the tidal cycle. Ordinate: clearances in colloidal graphite suspensions: ○ *Mytilus*, group 1; × *Mytilus*, group 2; ● *Mytilus*, group 3. The projections on the horizontal axis indicate the time intervals in hours between the measurements of clearances and the nearest low or high tides.

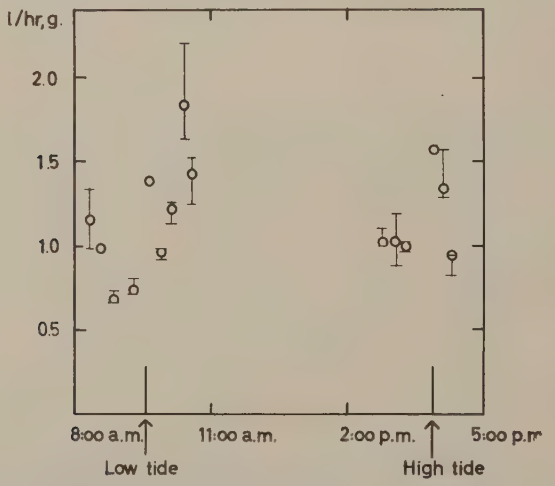

Figure 8. Relationship between water transport in *M. edulis* and the tidal cycle. The vertical bars indicate range of clearances of colloidal graphite, estimated as explained in the text p. 103.

made by Rao and the present writer are only partially comparable. In Rao's experiments, the mussels were most likely transporting water at reduced rates, at least at rates considerably lower than in the present experiments in which the mussels probably filtered at about the rates of undisturbed animals in natural environments (p. 108). Rao did not, therefore, investigate the relationship

between the phases of the tidal cycle and the natural, unrestricted, water transport. The rhythm in water transport found by him may be secondary to a rhythm in the sensitivity towards those factors in the laboratory environment that were responsible for the abnormally low water transport; as the laboratory environment was constant throughout the experiments, it follows that such a rhythm in sensitivity must result in a synchronous rhythm in the measured clearances.

Rates of water transport in *Mytilus* from different tidal levels

Segal, Rao, and James (1953) found that in *Mytilus californianus* the water transport, measured as clearances of colloidal graphite, was, at the same temperature, slower in animals from the upper tidal zone than in animals from the lower zone. No such difference was found in the present experiments on *M. edulis*. From Table 2 it is seen that mussels from the mid-tidal zone (groups 1 and 2) on an average cleared 1·19 and 1·65 l/hr./g, whereas mussels from the lowest level of the tidal zone (group 3) cleared 1·59 l/hr./g.

Pecten latiauratus

The results of the experiments with *P. latiauratus* are shown in Figure 9. Determinations of clearances and oxygen consumption were begun the day after the animals were brought into the laboratory. It is seen that the clearances were high in suspensions of diatoms, and medium or low in suspensions of

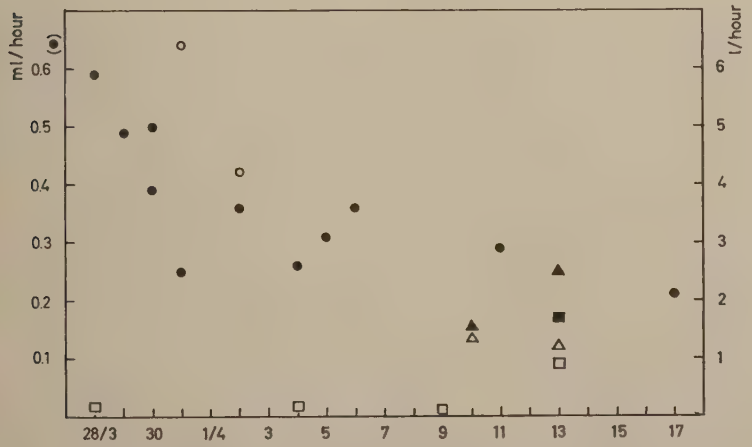

Figure 9. Rates of oxygen consumption (●) and clearances in a group of 4 specimens of *Pecten latiauratus*. Clearances were measured of diatoms (○) and of graphite in suspensions of freshly prepared (□) and aged (■) Aquadag, and of freshly prepared (△) and aged (▲) Prodag. Temp. 16–17°C. Abscissa: dates of experiments. The scallops were brought into the laboratory 27. March.

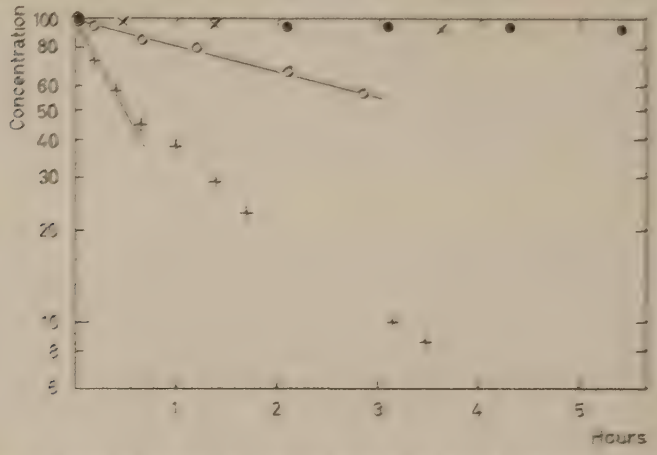

Figure 10. Rates of removal of colloidal graphite by *Pecten latissimus*: in suspensions of freshly prepared Aquadag (○) and Prodag (●) and × concentrations of suspensions of Aquadag and Prodag in control jars without scallops. Ordinate: concentration in per cent. of the initial concentration.

graphite. The graphite clearances were decreasing with time, except in the experiments yielding very low clearances. Typical examples are shown in Figure 10, from which it can also be seen that sedimentation of both Aquadag and Prodag was negligible in the absence of the scallops. Initial clearances of graphite were estimated as indicated in the figure. It is these estimates that have been used in Figure 9 as values for the clearances.

Due to the large size of the diatoms, the clearances in the diatom suspensions must approximate the absolute rates of water transport through the gills. The oxygen uptake declined rapidly during the first four days, and was probably decreasing throughout the experimental period. No well defined relationship, therefore, existed between rates of water transport and oxygen uptake; assuming a water transport of 5 l hr., the ratios between the rates increased from about 8 in the beginning to about 25 at the end of the experimental period.

It further appears from Figure 9 that Prodag suspensions were cleared faster than Aquadag suspensions, when suspensions of equal age were compared, and that aged suspensions were cleared faster than fresh suspensions. This is evident from the series of experiments made 13. April, where the clearance determinations were made in the order: fresh Prodag; fresh Aquadag; two hours old Prodag; two hours old Aquadag suspensions.

It is unlikely that the rates at which the *Pecten* transported water varied with the kind of suspension added to the animals. The appearance of the animals was the same whether diatom or graphite suspensions were added; and the turbulence produced at the water surface by the water pumping was not visibly weaker in the experiments yielding low than in those yielding high clearances. The low, but varying clearances in the graphite suspensions were therefore most likely due to a correspondingly low, but varying efficiency of particle retention in the gills.

The increase in particle size with the age of the suspension was most probably responsible for a large part of the variation found in the efficiency of particle retention. However, a variable porosity of the gills was probably also at play. Freshly prepared Aquadag suspensions were thus mostly cleared at rates of 0·1 to 0·2 l hr., indicating that only some few per cent. were retained of the 1–2 μ graphite particles: but in one experiment a fresh Aquadag suspension was cleared at a rate of 0·9 l hr. The fraction of 1–2 μ particles retained in this experiment was therefore apparently several times higher than in the experiments mentioned above.

Discussion and Conclusions

Lamellibranchs are very sensitive towards changes in their environment; even slight chemical or mechanical stimulation may cause partial or complete closure of the valves, and thus partial or complete stoppage of the water transport. Obviously, experimental determinations of the water transport are not practicable without some deviation from the normal environment and some disturbance of the animals. The rates of water transport obtained in the present study should therefore be critically evaluated in order to see how closely they correspond to rates in undisturbed animals.

In the laboratory at Mount Desert Island, the undisturbed mussels, both small and large, in the glass jars and in the big aquarium were open and looked like mussels observed in the sea outside the laboratory. As mentioned above, very young mussels and barnacles grew considerably during the period of experiments, so that the running water from the tank of the laboratory evidently contained enough food for maintenance and growth. Consequently, when undisturbed and in running sea water, the mussels used for experiments presumably transported water at normal rates through gill filters of normal porosity. However, during an actual experiment, the circulation was stopped. When this happened large mussels, more than 5 cm long, soon slightly retracted the mantle edges. The siphons would then gradually retract and the valves close, though not necessarily completely, and they often remained half-open for many hours. Small mussels, less than about 4 cm long, generally did not begin closing the valves until some hours after the circulation was stopped. A few minutes after the running water was again started, both small and large mussels were normally open.

The effect on the mussels of stopping the circulation was not due to temperature changes: the temperature in the glass jars remained practically the same as in the large aquarium, where the sea water was continuously running. Neither was the reaction likely to be caused by the absence of the water movements produced by the running water, because strong water movements were produced by the mussels themselves. Further, the long latency and the slowness of the reaction indicate a slowly growing stimulus, such as might arise from the accumulation of excretory products in the water, or from the progressive extraction from the water of some factor necessary for maintaining normal water transport. A stimulating factor is assumed to regulate the normal pumping activity of the oyster *Crassostrea virginica* in the Mexican Gulf (Collier, Ray, Magnitzky, and Bell, 1953).

Rapid closure of the valves in large mussels confined to a small volume of non-flowing water was also observed in *Mytilus* at the Scripps Institution of

Oceanography, California, at the Marine Biological Laboratory, Woods Hole, Massachusetts, and at the Plymouth Laboratory, England (Jørgensen, 1949). Thus, generally speaking, mussels are the more sensitive towards changes in their environment the larger they are. So far, we have only found it possible to use small individuals in the determinations of rates of water transport in undisturbed mussels by means of the clearance method, because only mussels less than 4–5 cm in length would remain normally open after stoppage of the running water for long enough to allow determinations of clearances.

Water transport

Even when exercising the greatest care, clearance experiments could not be performed without the mussels reacting slightly; and sometimes conspicuously by partially retracting the siphons and closing the valves. In order to see what effect the reactions had on the rates of water transport, it was attempted to correlate these with the appearance of the mussels.

In undisturbed mussels, the tentacles along the edges of the inhalent siphon are mostly turned outward, away from the aperture of the siphon; but when the suspensions were added, the tentacles of almost all the mussels usually reacted by moving a little towards the aperture of the siphon; and generally the tentacles remained pointing against the inhalent current during the experiment. This reaction mostly took place without visible closure of the valves or reduction in size of the apertures of the siphons. Sometimes, however, the valves did visibly close, apparently affecting the water transport. Thus, mussels noted to have reacted by retracting the siphons and closing the valves a little during the experiments were found to have cleared only 1·14 l/hr./g (range 0·98 to 1·35, 8 experiments performed on *Mytilus* group 3), against 1·59 l/hr./g in experiments in which, at the most, the reaction of the tentacles were observed.

Half-closed mussels, as observed during the long-term experiments on clearance of haemoglobin and haemocyanin, cleared graphite suspensions at an average rate of 0·34 l/hr./g (range 0·18–0·66 l/hr./g, 6 experiments on *Mytilus* group 2), or one fifth of the rate of the normally open mussels (Table 2).

A small, but unmistakable reduction in lumen of the siphons, thus reduced the rate of water transport by some 30%. A reaction confined to a change in orientation of the tentacles presumably had an even smaller effect: the measured rates of water transport therefore probably approximate the true filtration rates of undisturbed mussels.

The rates of water transport determined in the present and in previously published investigations were obtained in experiments of short duration, yet they probably correspond closely to the true daily average rates of filtration in permanently submerged mussels. The rate of 1·48 l/hr./g obtained with *M. edulis* in Maine results from measurements made on 33 mussels over a total period of 592 minutes; or one mussel over a period of 106 hours. The value therefore represents the average water transport over a period of more than four days by an average mussel, representing 33 randomly chosen individuals.

In Figure 11, the values of water transport in *M. edulis* obtained in the present study are compared with previously published values for *M. edulis* and other lamellibranchs. All rates have been expressed per gramme wet weight of the soft tissues; when sizes but not weights of the experimental animals were stated,

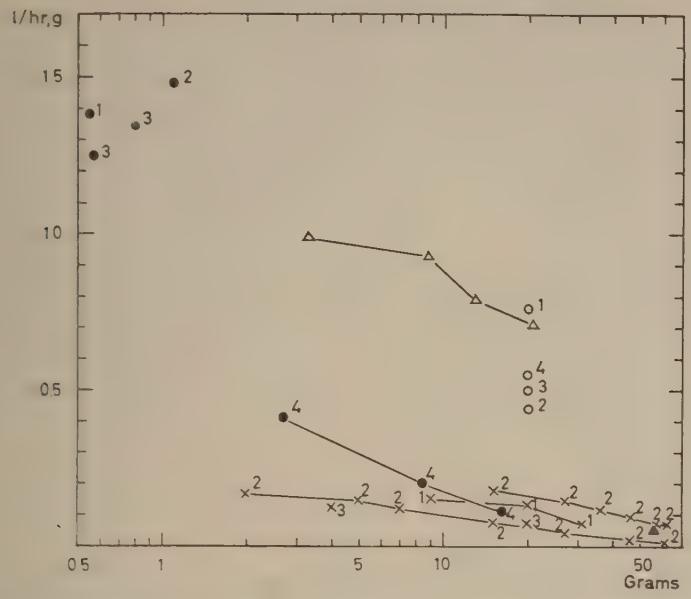

Figure 11. Relationship between rate of water transport and wet weight of soft parts in various lamellibranchs.

Crassostrea virginica

○[1] Loosanoff and Nomejko (1946). Temp. 19–26°C. Water transport directly measured.
○[2] Loosanoff (1958). Temp. 16–28°C. Water transport directly measured.
○[3] Galtsoff, *et al.* (1947). Temp. 10–28°C. Water transport directly measured.
○[4] Jørgensen (1952). Temp. 21–22°C. Clearance of colloidal graphite.

Mytilus edulis

●[1] Present study. California. Temp. 14–15°C. Clearance of colloidal graphite.
●[2] Present study. Maine. Temp. 13–14°C. Clearance of colloidal graphite.
●[3] Jørgensen (1949). England. Temp. 16–19°C. Clearances of flagellates and diatoms. Weight estimated from curve in Fig. 12.
●[4] Willemsen (1952). Holland. Temp. 12–15°C. Clearance of silt. Weight estimated from curve in Fig. 12.

Mytilus californianus

×[1] Fox, Sverdrup and Cunningham (1937). Temp. 19–23°C. Clearances of calcareous mud or $CaCO_3$. Weight estimated from Fox and Coe (1943) Table I.
×[2] Rao (1953). Temp. 10 and 20°C. Mussels from Los Angeles. Clearance of colloidal graphite.
×[3] Segal, Rao and James (1953). Temp. 16°C. Mussels from the middle intertidal zone. Clearance of colloidal graphite.

Pecten irradians

△ Chipman and Hopkins (1954). Temp. 22–26°C. Clearances of flagellates and diatoms.

Amphidesma ventricosum

▲ Rapson (1952, 1954). Clearance of diatoms.

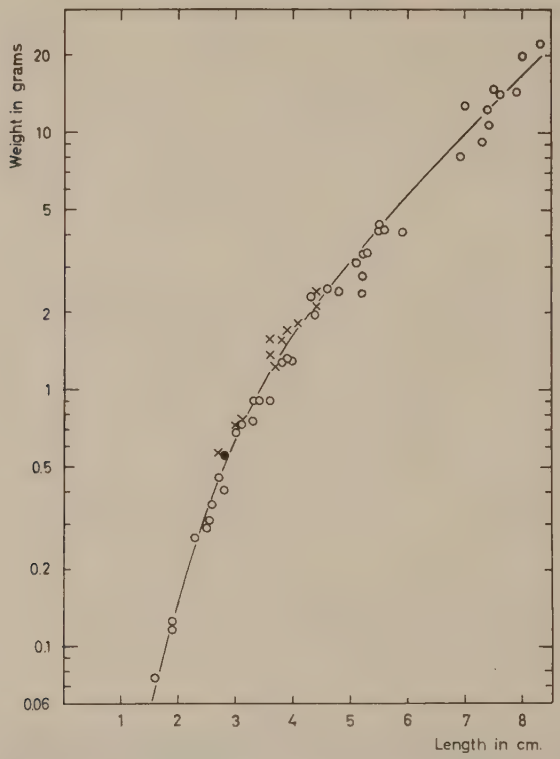

Figure 12. Relationship between length in cm and wet weight of soft parts in grammes in *Mytilus edulis*: ○ from Denmark; × from Maine; ● from California (average of four specimens).

the weights have, where possible, been estimated. All experiments on *Crassostrea virginica* have been made on adult individuals; generally the weight is not stated, but is here assumed to have been 20 g. The weights of *M. californianus* used in the experiments of FOX, SVERDRUP, and CUNNINGHAM (1937) were estimated from the relationship between length and weight found by FOX and COE (1943); weights of *M. edulis* used by JØRGENSEN (1949) and WILLEMSEN (1952) were read from the curve in Figure 12, based on measurements of weight and length of mussels from Denmark and the U.S.A. The rates of water transport calculated on the basis of estimated weights are of course not strictly comparable with the rates calculated on the basis of measured weights. However, the rates of water transport in *M. edulis* found by the various authors vary so much that only an insignificant part of the variation can possibly be due to inaccurate estimates of the weight.

Large mussels have been found to transport water at much lower rates than oysters and scallops of comparable weight, and than smaller mussels. However, as all the rates of water transport in mussels were measured by means of the

clearance method, which in the hands of the present author yielded normal rates only when applied to small mussels (see p. 107), the low values obtained in the larger mussels must be suspected not to represent normal values.

The variations found in the rates of water transport in the oyster may to a great extent be due to the use of the assumed weight of 20 g of all the experimental animals; within the accuracy of the determinations, the rates of water transport were independent of the method used, whether direct (GALTSOFF *et al.*, 1947; LOOSANOFF, 1958; LOOSANOFF and NOMEJKO, 1946) or indirect (JØRGENSEN, 1952).

Amphidesma ventricosum transported water at low rates. During the experiments the animals were placed in a jar with sand; sea water rich in phytoplankton was added, and rate of removal of *Chaetoceros* colonies from the suspension was followed. The clearance was thus apparently measured under natural conditions; and the clearance presumably approximates the rate of water transport because the big *Chaetoceros* colonies are unlikely to pass through the gills. However, it is stated that only one out of several tests was successful, so more experiments are necessary to decide whether the calculated rate is normal. Beforehand, relatively low rates of water transport are likely to be expected in *A. ventricosum* which occupy localities especially rich in phytoplankton (RAPSON, 1952, 1954).

Clearances have been measured in a few other lamellibranchs: *Venerupis pullastra* cleared suspensions of iron oxide at low rates (QUAYLE, unpublished); and so did *Venus mercenaria* suspensions of a minute green alga and a small diatom (RICE and SMITH, 1958). In neither instance was the efficiency of retention of the particles stated, so the rates of water transport are not known.

Porosity of the gills

In the present and in previous experiments it was constantly found that particles from one to a few microns in size were almost completely retained during one passage of the suspension through the gills, even under adverse conditions where the mussels cleared graphite at about one fifth the normal rate (JØRGENSEN, 1949; JØRGENSEN and GOLDBERG, 1953). Contrary to these findings, TAMMES and DRAL (1955) observed widely varying retention of particles less than 30–40 μ. Thus, the retention of 7–8 μ blood corpuscles, and other particles of similar sizes, varied from 0 to 98%; and from 0 to 50% of 1·5–2·5 μ flagellates.

This difference in result can probably be explained by differences in experimental technique. In TAMMES and DRAL's experiments, the mussels were furnished with a plastic tube in the exhalent aperture and embedded in plaster of Paris. It therefore appears that only undisturbed mussels efficiently retain particles down to about 1 μ: when exposed to conditions that are too artificial, the gills become more, but variably, porous.

In the oyster, *Crassostrea virginica*, contradictory results have likewise been obtained in experiments on particle retention. LOOSANOFF and ENGLE (1947) found very varying retention of microorganisms of various sizes. The percentage of the 5 μ cells of *Chlorella* sp. retained by the gills varied from 0 to 85; usually more than 50% passed through the gills; the percentage of 60 μ cells of *Euglena viridis* varied from 15 to 80. The efficiency of retention was independent of the cell concentration even at concentrations so low that the rate

of water transport was unaffected. Jørgensen (1952) however, in experiments on clearances of graphite suspensions, found that particles of sizes down to a few microns were effectively retained, whereas the 1–2 μ particles of freshly prepared suspensions largely passed through the gills.

Again, these different results probably arise from differences in technique. The measurements of water transport by means of the direct method implies a separation of the inhalent and exhalent currents, achieved by wrapping round the oyster a piece of dental rubber dam to form a cone completely enclosing the exhalent aperture. In contrast with the clearance method, this direct method thus necessitates considerable handling of the experimental animals. Therefore, the efficiency of retention found by means of the clearance method probably approximates more closely to the natural efficiency than does the direct method.

As mentioned already, the direct and indirect method did not provide significantly different rates of water transport. Thus, the experiments on mussels and oysters show that porosity of the gills and rates of water transport can vary independently of each other, as already observed in the mussel by Tammes and Dral (1955).

The experiments on *Pecten latiauratus* revealed a low, but varying retention of colloidal graphite of various particle sizes. However, the scallops survived for only about a month in the laboratory, and they were very soon after arrival probably adversely affected by the laboratory conditions. Considering how easily the experimental conditions can change the properties of the gills, the gill filters may have been abnormally porous in the experiments; in order to get reliable determinations of the normal gill porosity, further experiments are needed on scallops living in a tolerable environment.

So far, the presumably normally functioning gill was found to retain particles efficiently down to about one or a few microns in *Crassostrea virginica*, *Mytilus edulis*, and in the tiny *Lasaea rubra* (Ballentine and Morton, 1956). It is perhaps likely that under natural conditions filter feeding lamellibranchs, generally, will be found to extract almost completely all particles from the water passing the gills down to the sizes of bacteria and other minute organisms. However, in *Mytilus edulis* big molecules such as lobster haemocyanin largely passed through the gills that almost completely retained about 1 μ particles. Also *Lasaea rubra* retained inefficiently the big molecules of *Arenicola* haemoglobin (Ballentine and Morton, 1956), but in these experiments particles just above the critical size were not present in the suspensions simultaneously with the haemoglobin, so it is not definitely known whether or not the presence of the haemoglobin itself changed the porosity of the gills. Nevertheless present evidence suggests that dissolved and colloidal organic matter in the sea may be only slightly accessible to even undisturbed, normally feeding lamellibranchs.

Most investigations on the functioning of the lamellibranch gill in feeding have been made on the exposed gills of individuals with one valve and mantle removed. The literature on feeding mechanisms in lamellibranchs will not be discussed here; reference is made to the review by Jørgensen (1955) and later work by Purchon (1955, 1956a, b). Yet it should be emphasized that the fact that a low and constant porosity of the gills was found only in undisturbed mussels and oysters clearly demonstrates the necessity of supplementing the observations made on feeding mechanisms in mutilated animals by observations on normal and undisturbed animals, as already strongly stressed by Mac Ginitie (1941).

Table 3

Relationship between rate of water transport and oxygen consumption in lamellibranchs

Species	Age and size	Locality	Filtration rate l/ml O_2 consumption
1. *Crassostrea virginica*	Adult	Woods Hole, Mass.	16
2. *Ostrea edulis*	Veliger		40, 15
3. *Pecten latiauratus*	Adult	Mission Bay, Calif.	17 (8–25)
4. *Pecten irradians*	Half-grown	Off Beaufort, N. C.	9·5
5. *Lasaea rubra*	Adult	Tidal Zone, Plymouth	2 (1–4)
6. *Mytilus edulis*	Young		
a)	0·55 g, soft parts	Tidal Zone, off La Jolla, Calif.	15
b)	1.1 g, soft parts	Tidal Zone, Mount Desert Island, Maine	13
c)	0·055 g, soft parts	Off Plymouth	8·5
	0·57 g, soft parts	Off Plymouth	8·0
	0·80 g, soft parts	Off Plymouth	9·6

1. Jørgensen (1952). Rates of filtration and oxygen consumption measured on the same individuals. Temp. 21–22°C.
2. *Ostrea* veliger, 200 μ in length, filtered 27 mm³/hr. at 20–22° (Bruce, Knight, and Parke, 1940; Jørgensen, 1943); veligers 218–279 μ in length, 19 mm³/hr. (Walne, 1956). *Mytilus edulis* veligers of the same sizes consume 66 $\times$ 10^{-5} and 130 $\times$ 10^{-5} mm³ O_2/hr. (Zeuthen, 1947). As *Mytilus* and *Ostrea* veligers of these sizes are similar in shape and organization, it was considered possible to apply the values for oxygen uptake in *Mytilus* in the calculations.
3. Present study. Temp. 16–17°C.
4. Individuals, 6–13 g wet weight of soft parts, filtered 0·86 l/hr./g at Beaufort, N. C. (Chipman and Hopkins, 1954; 22–26°C) and consumed about 0·09 ml O_2/hr./g at Woods Hole, Mass. (v. Dam, 1954; 21°C).
5. Ballentine and Morton (1956): Morton, Boney, and Corner (1957). Measurements of filtration and oxygen consumption on animals from the same locality, but not on the same individuals.
6. a) Present study. Rates of filtration and oxygen consumption measured on the same individuals. Temp. 14–15°C.
   b) Filtration rate; present study. Temp. 13–14°C. Oxygen consumption, at 16°C, from Zeuthen (1947), Fig. 35.
   c) Filtration rate, Jørgensen (1949). Temp. 16–19°C. Oxygen consumption, at 16°C, from Zeuthen (1947), Fig. 35.

Relationship between water transport and oxygen consumption

The rates of water transport must be adjusted on the one hand to the food requirements of the lamellibranch in question, and on the other to the concentration, size, and value of the food particles suspended in the surrounding water. Further, the amounts of food actually utilized must vary, within limits, with the concentration of available food.

In order to elucidate these complex interrelationships it is important to know how rate of water transport may vary in relation to oxygen consumption which provides a measure of the minimal food requirements. Table 3 compiles available data, expressed as litres of water filtered for each ml of oxygen taken up.

It is seen that in adult oysters and scallops, and in oyster veligers and young mussels, the ratios between rates of water transport and oxygen uptake are not significantly different. As young, fast-growing lamellibranchs utilize about

twice as much of the absorbed nutrients for growth as for combustion, correspondingly higher rates of water transport relative to oxygen consumption might have been expected in young than in adult lamellibranchs which only utilize a small fraction of the absorbed nutrients for growth (Jørgensen, 1952). However, further experiments are needed to determine whether water transport in relation to oxygen consumption does or does not vary with growth rate or age.

In *Lasaea rubra*, the ratio between rates of water transport and oxygen consumption was only about a quarter the value calculated for *M. edulis* from the same locality (see Table 3: 5 and 6c), but before discussing possible ecological and physiological consequences of this difference, it should be ascertained to what extent the results are influenced by the techniques applied in measuring water transport and oxygen consumption.

In an extensive study, Loosanoff (1958) found no significant difference in the rates of water transport at temperatures varying from 16 to 28°C. From the data presented in Figures 61 and 62, and Table 52 in the paper of Galtsoff *et al.* (1947) it appears that the rates of water transport varied independently of the temperature within the even wider range of 10 to 28°C. As the rate of oxygen consumption increases with the temperature, rates of water transport in relation to oxygen consumption must fall proportionally. On average, the oxygen consumption in various species of oysters were found to be tripled when the temperature rose from 10 to 28°C, and doubled when it rose from 16 to 28°C (Gaarder and Eliassen, 1954; and Pedersen, 1947; *Ostrea edulis*: Nozawa, 1929; *O. circumpicta*: Mitchell, 1914; see also Galtsoff and Whipple, 1931; *Crassostrea virginica*). Consequently, the feeding conditions are the poorer the higher the temperature within the natural temperature range in which *Crassostrea virginica* lives; a result that invites further investigations.

Summary

1. As a contribution to the study of normal feeding in lamellibranchs, rates of water transport and porosity of the gill filters were determined in *Mytilus edulis* (L.) and *Pecten latiauratus* Conrad under experimental conditions that were hoped to be compatible with normal feeding behaviour.

2. The rates of water transport were determined from the rates at which suspensions were cleared of particles that were approximately completely filtered from the water passing the gills. In the mussel, suspensions of colloidal graphite (Aquadag) served the purpose; in the scallop, suspensions of the diatom *Asterionella japonica*.

3. The degree of retention of particles not completely filtered from the water passing the gills was determined from the rates at which suspensions of such particles were cleared, in relation to the clearances of completely retained particles.

4. Young mussels, wet weight of soft parts about 1 g, efficiently retained 1–2 μ particles of colloidal graphite, the average size of particles in freshly prepared suspensions. Protein molecules, haemocyanin from the blood of the lobster *Homarus americanus*, and haemoglobin from the blood of the dogfish *Acanthias squalus*, were inefficiently retained: the degree of retention could not be accurately determined, but was at most a few per cent.

5. The scallops inefficiently retained colloidal graphite.

6. In the young mussels sampled in the tidal zone, the rate of water transport in undisturbed animals was about 1·5 litre per hour and gramme wet weight of the soft parts, at 13–14°C. The rates of water transport, as measured under the standardized laboratory conditions, varied neither with the tidal cycle nor with the level of the tidal zone from which the mussels originated.

7. Preliminary data were obtained to elucidating the complex interrelations between food requirements and rates of water transport, by determining in the same individuals rates of both water transport and oxygen consumption. The mussels were found to filter about 14·5 l of water for each ml of oxygen taken up. In the scallops, oxygen consumption was decreasing during the experimental period, so no well defined relationship existed between rates of water transport and oxygen consumption. The ratios between litres of water transported and millilitres of oxygen consumed increased from about 8 in the beginning to about 25 at the end of the experimental period.

8. It is concluded that the porosity of the gill filters and rates of water transport obtained in the experiments with the young mussels probably closely correspond to the porosity and rates of water transport in undisturbed animals under natural conditions; whereas the high porosity found in the scallops may be due to adverse laboratory conditions.

9. It is suggested that the high and varying porosity recorded in the literature on mussels and oysters is typical of disturbed animals, and that, generally, undisturbed filter feeding lamillibranchs will efficiently retain particles down to one or a few microns in size.

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Temperature, Growth, and Mortality – The Pacific Cockle

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Introduction

In considering the causes of LEE's phenomenon in Georges Bank haddock, TAYLOR (1958a) suggested that a differential mortality rate associated with rate of growth could account for at least a part of the phenomenon. The concept of a relation between longevity and growth-rate is not new (e.g., PEARL, 1928; MCCAY, 1933). The idea that growth-rate may introduce a mortality rate operative over the life span appears more difficult to accept. If, however, this is true, estimations of the natural mortality rate in fish population dynamics may have been facilitated.

This paper adds yet another example of a species whose growth appears to be quantitatively related to environmental temperature and shows that longevity and natural mortality estimated from growth characteristics are in very good agreement with independent estimates obtained from the age structure of unexploited populations of the species.

WEYMOUTH and THOMPSON (1931) present growth data for the Pacific cockle, *Cardium corbis*, at 8 localities ranging from Oregon to Alaska. Treating these data in the same manner as for the Pacific razor clam (TAYLOR, 1959) but excluding lengths at ages 9 and 10 at Kake, Alaska, and at ages 1 and 11 at Snug Harbor, Alaska (because they are aberrant and based on only 1 or 2 cockles) I have calculated the growth parameters of BERTALANFFY's (1938) equation:—

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \tag{1}$$

the Bertalanffy coefficient of anabolism:—

$$E = L_\infty \times K \tag{2}$$

and an index of longevity (TAYLOR, 1958a, 1958b, 1959):—

$$A_{0.95} = t_0 + \frac{2.996}{K} \tag{3}$$

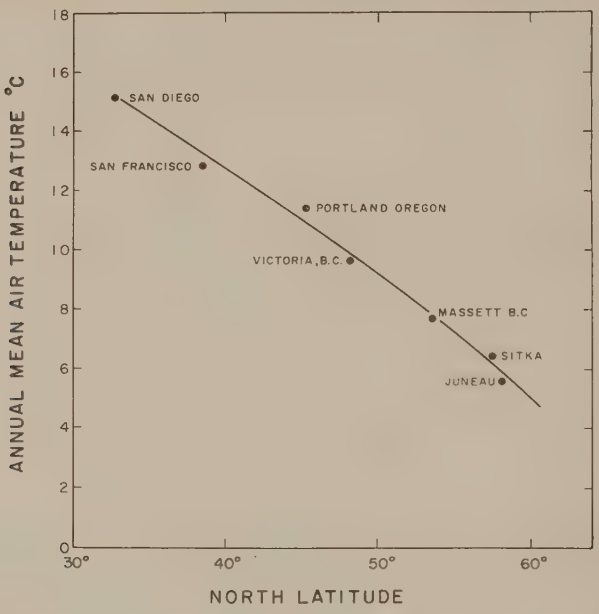

Figure 1. Smoothed curve of air temperature against latitude, San Diego, California to Juneau, Alaska.

Estimation of Air Temperatures

Figure 1 (from TAYLOR, 1959) is used to estimate the mean annual air temperatures at the localities listed in Table 1 by reading the temperature from the smoothed line which corresponds to the latitude of each locality. It is known that air temperatures along the west coast of North America are generally indicative of coastal water temperatures (ROUNSEFELL, 1930; HUBBS, 1948; KETCHEN, 1956). For the period during which WEYMOUTH and THOMPSON were collecting these data for the Pacific cockle (1920's), more air temperature information is available than inshore surface water temperatures. The close correspondence of mean annual surface water temperatures and air temperatures is shown for certain localities and periods in Table 2. These means differ somewhat from those shown in Table 1 because they are not based on the same period of years.

Relation of K to mean air temperature

Figure 2 shows the logarithms of K at the eight localities of Table 1 plotted against mean annual air temperature. The regression of log K on temperature is:

$$\log K = 0{\cdot}0632\,T - 0{\cdot}9433 \qquad (4)$$

with correlation coefficient 0·887. The 1% level of significance for 6 degrees of freedom is 0·834 (see discussion).

Table 1

Growth parameters of *Cardium corbis*, Oregon to Alaska, and estimated mean annual air temperatures

Locality	Latitude N	Est. mean air temp. °C	K	L_∞	E	t_0	$A_{0\cdot95}$
Tillamook, Oregon	45°31′	10·9	0·54	8·32	4·48	0·48	6·03
Copalis, Washington	46°58′	10·3	·62	7·70	4·76	0·52	5·35
Kake, Alaska	56°55′	6·4	·26	9·56	2·52	–	–
Cordova, Alaska	60°27′	4·9	·24	10·21	2·40	0·89	13·37
Constantine Harbor, Alaska	60°35′	4·8	·26	7·67	2·01	0·80	12·32
Snug Harbor, Alaska	60°10′	5·0	·28	10·25	2·86	–	–
Kukak Bay, Alaska	58°30′	5·5	·25	11·37	2·82	·88	12·86
Port Moller	56°00′	6·8	·21	8·61	1·82	0·78	15·05

Table 2

Comparison of mean annual air and surface water temperatures at certain localities

Locality	N Lat.	Period	Mean annual temperature °C Air	Surface water
San Diego, Calif.	32°42′	1921–1930	16·6[1])	–
Scripps Pier, La Jolla, Calif.	32°52′	1921–1930	–	17·0[2])
San Francisco, Calif.	37°48′	1922–1931	13·2[1])	14·1[3])
Seattle, Wash.	44°37′	1922–1931	11·0[1])	11·0[3])

[1]) U.S. Weather Bureau, Climatological Data.
[2]) Data supplied through courtesy of Scripps Institution of Oceanography, La Jolla, California.
[3]) U.S. Coast and Geodetic Survey, "Surface Water Temperatures, Coast and Geodetic Survey Tide Stations, Pacific Coast." TW–2, 1945.

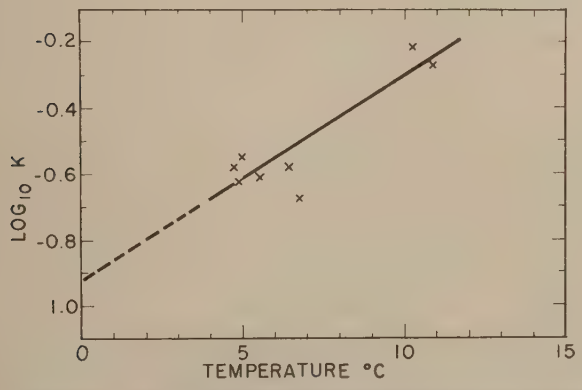

Figure 2. Regression of log K on estimated air temperature for the Pacific cockle at the eight localities shown in Table 1.

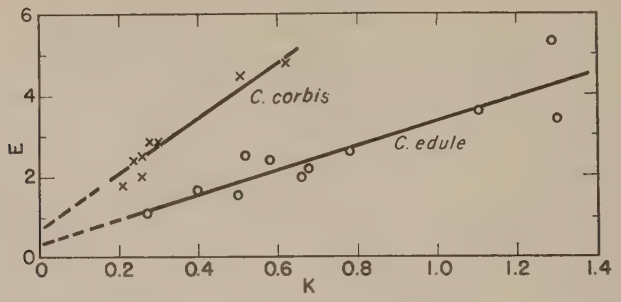

Figure 3. Regression of E on K for *Cardium corbis* compared to that for *Cardium edule*.

Relation between E and K

As with various other fish and shellfish, the relation between E and K appears linear (Figure 3) with regression equation

$$E = 6{\cdot}760\ K + 0{\cdot}715$$

Figure 3 also compares the regression of E on K for *Cardium edule* (TAYLOR, 1959), the latter being based on growth data published by COLE (1956).

Longevity

WEYMOUTH and THOMPSON (1931, Table 2) compute a "maximum age" for *Cardium corbis* for 6 of the 8 localities in Table 1. They state: "On a survival curve for each locality the age was located at which 5 percent of the clams passing through the first winter were still alive. This was taken as the maximum age." Figure 4 compares the maximum age thus computed with the $A_{0{\cdot}95}$ of Table 1.

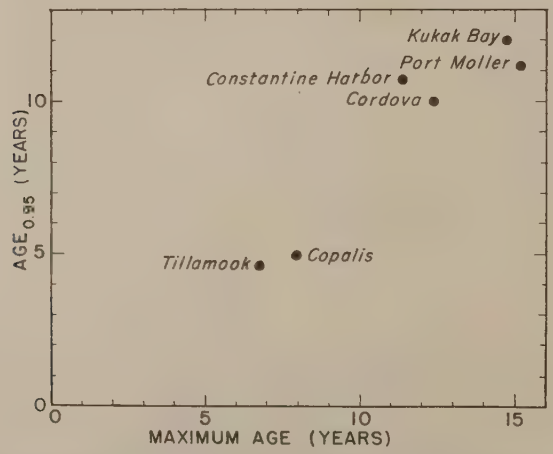

Figure 4. Comparison of maximum age estimated from age composition by WEYMOUTH and THOMPSON to $A_{0{\cdot}95}$ estimated from growth parameters.

Table 3

Estimates of the natural mortality coefficient, M, obtained from age composition data for *Cardium corbis* compared to M's estimated from $A_{0.95}$

Locality	M estimated from age composition	M estimated from $A_{0.95}$
Tillamook, Oregon	0·525±0·023	$0{\cdot}497^{+0{\cdot}173}_{-0{\cdot}075}$
Copalis, Washington	0·594±0·056	$0{\cdot}560^{+0{\cdot}180}_{-0{\cdot}051}$
Cordova, Alaska	0·286± ·007	$0{\cdot}224^{+0{\cdot}106}_{-0{\cdot}025}$
Constantine Harbor, Alaska	0·384±0·033	$0{\cdot}243^{+0{\cdot}053}_{-0{\cdot}015}$
Kukak Bay, Alaska	0·258±0·012	$0{\cdot}233^{+0{\cdot}035}_{-0{\cdot}006}$
Port Moller, Alaska	0·225±0·005	$0{\cdot}199^{+0{\cdot}087}_{-0{\cdot}056}$

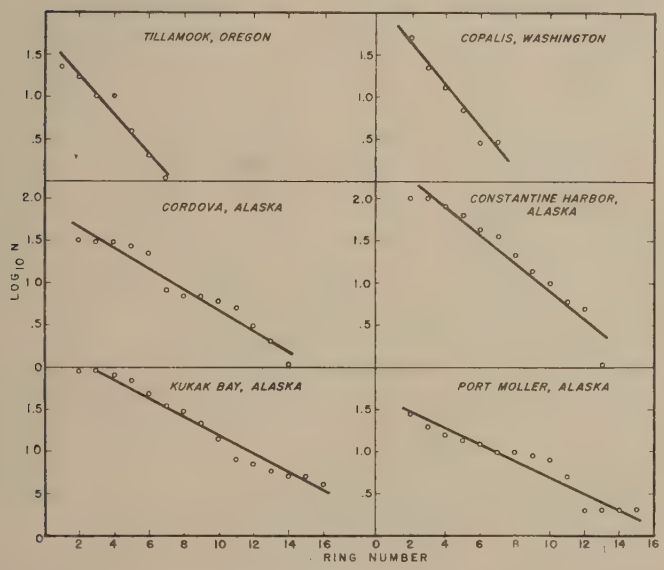

Figure 5. Regressions of the logarithm of numbers of cockles on age, as given by number of rings, at different localities.

Natural Mortality

The *Cardium corbis* populations shown in Table 1 were essentially unexploited at the time the growth data were collected. Weymouth and Thompson state (1931, p. 633): "Although the cockle is very abundant in many localities and is an excellent food mollusk, it has never attained commercial importance because of its poor keeping qualities and small edible content. The local markets absorb small quantities, and many are used by crab fishermen for bait. Attempts have been made to can the cockle, but have not met with success."

WEYMOUTH and THOMPSON consider the numerical abundance at each age (1931, Table 3) as representative of the population, with the exception of the smaller samples taken at Kake and Snug Harbor, Alaska.

Computing the regression of the logarithm of numbers on age (using ages 1–7 at Tillamook; 2–7 at Copalis; 2–14 at Cordova; 2–13 at Constantine Harbor; 2–16 at Kukak Bay; and 2–16 at Port Moller), estimates of the natural mortality coefficient, M, were obtained, together with standard errors. The goodness of fit of these regressions may be judged from Figure 5.

Alternatively, M was estimated by dividing $-\log_e(1 - p)$ by A_p, in this case 2·996 by $A_{0\cdot95}$ (TAYLOR, 1959). Estimates of M with their standard errors are compared in Table 3.

Discussion

The slope of regression equation (4) and its associated correlation coefficient depend entirely on two values of K above 10°C (see Table 1 and Figure 1). Since the correlation surface is not normal, the probability levels are subject to question. The reader must, then, judge the validity of the relation between temperature and K in the light of similar relations found for the cod and razor clam (TAYLOR, 1958b, 1959).

Relations between growth parameters and temperature bearing as they appear to on related problems of longevity and mortality suggest certain new methods of approaching some of the thornier problems of fishery biology and population dynamics. These methods are untried, indeed unverified, but nevertheless promising.

By and large, we must assume an average response for each species to the environment and an average response for the individuals within a species. Individual variations must occur. In the haddock, for example, certain growth parameters appear associated with size at age 1, the latter sizes being more or less normally distributed (TAYLOR, 1958a, Table IV, p. 245).

On the other hand, to apply such methods, size and age data must be suitably graduated by the Bertalanffy equation, more particularly by the regression of L_{n+1} on L_1 (WALFORD, 1946). It is not at all unusual to find growth data in which the slope of the latter regression is very close to or greater than 1·0 or in which the value of t_0 is greatly in excess of - 1·0. In such instances, one must conclude either that the animal does not grow in a manner described by the Bertalanffy equation or that the growth data themselves are in error. The effect of an error in estimating the time at which the first annulus in hard parts is formed on the value of t_0 may be readily seen by treating the size at age 2 as if it were age 1 and so on.

Air temperatures, especially when estimated from latitude, are at best crude measures of environmental temperature. The air temperature at Port Moller, Alaska (Table 1), for example, is probably lower than the latitude of the location would indicate since Port Moller lies on the northern side of the Alaskan Peninsula on the Bering Sea.

The regression of log K on temperature for the three species, cod, razor clam, and Pacific cockle are as follows:—

Cod	$\log K = 0{\cdot}0768\ T - 1{\cdot}4380$
Razor clam	$\log K = 0{\cdot}0849\ T - 1{\cdot}0987$
Pacific cockle	$\log K = 0{\cdot}0632\ T - 0{\cdot}9433$

The slopes of these regressions do not differ significantly. They are, however, approximately three times as great as, and differ significantly from, what we would expect for a Q_{10} of 2 or 3, say. (Q_{10} is the ratio of the rate of activity at one temperature to the rate at a temperature 10°C lower.)

A temperature-determined K, linearly related to E, determines the maximum size, L_∞. One may ask what happens to an animal at or near L_∞ if the average environmental temperature increases or decreases by one or more degrees centigrade?

If the temperature increases, K increases, $A_{0\cdot95}$ decreases, and the animal finds itself larger than the L_∞ defined by the conditions of the new environment. In terms of the concepts behind the Bertalanffy growth equation, the animal has attained a body volume now larger than the functional surface area can support.

One readily sees from equation (1) that a temperature change at any time amounts to a displacement of all animals from the growth curve defined by the temperature conditions of the former environment. Assuming that there cannot be negative growth, that t_0 is fixed during the first year of life and that the temperature change defines a new K and a new L_∞, the only remaining parameter which can be changed to make the equation balance is t. A change in t to satisfy the equation can only be interpreted as a change in the physiological age of the animal. Thus, displacements from the growth curve brought about by temperature changes must be regarded as having changed the physiological age of the animal with reference to its environment.

Calculations readily show that such "time" displacements are relatively slight for the younger and smaller animals over a wide range of temperatures, perhaps explaining the commonly-observed resilience of young animals to extremes of temperature. For animals at or near L_∞ changes amounting to only fractional degrees centigrade result in large "time" displacements. At intermediate sizes, the displacement depends on the amount of temperature change.

These results suggest a "trigger mechanism" for mass mortalities of animals. Extensive mortalities brought about among the larger animals by relatively slight temperature changes may introduce secondary bacterial or fungus diseases which extend to all sizes in the population. This hypothesis would explain many of the puzzling aspects of mass mortalities, especially those where a "causative" organism does not always cause mortality by its mere presence. The possibility that the herring fungus disease, *Ichthyosporidium hoferi* becomes widespread in 18-year cycles (FISH, 1934) even though the fungus is always present in herring populations (SCATTERGOOD, 1948) is suggestive in this respect.

Summary

Growth parameters of the Pacific cockle, *Cardium corbis*, are shown to be quantitatively associated to mean air temperatures. Values of E and K follow a linear trend different from that of *Cardium edule*. Longevity, estimated as $A_{0\cdot95}$, is in proportion to the maximum age as estimated by WEYMOUTH and THOMPSON. Estimates of natural mortality from the parameter $A_{0\cdot95}$ are in very good agreement with similar estimates based on the observed age compositions of unexploited populations of the cockle.

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Review

Ciba Foundation Colloquia on Ageing. Volume 5. The Lifespan of Animals. J. & A. Churchill Ltd., 324 pp. London, 1959. £2·8.

This volume contains 18 contributions concerning various aspects of ageing in animals, ranging from *Drosophila* to man. Readers of the *Journal du Conseil* will be most interested in the three contributions concerning fishes, and with the discussions following these and some other articles.

R. F. NIGRELLI—"Longevity of fishes in captivity, with special reference to those kept in the New York Aquarium"—tabulates the maximum number of years which various species have survived in various major aquaria. A sterlet (*Acipenser ruthenus*) at Amsterdam leads the field by several lengths, with 69 years. Next is the Frankfort carp that survived 38 summers, and may have prompted one of ALDOUS HUXLEY's more gruesome fables. At NIGRELLI's own New York aquarium a bowfin (*Amia*) and a longnose gar (*Lepisosteus*) divide top honours at 30 years, while a striped bass (*Roccus*) leads the saltwater division with 24 years. The only general conclusions might be that large fish usually live longer than small ones, and that freshwater fish survive better in captivity than saltwater ones, the latter perhaps because of greater difficulty in maintaining a suitable environment. Ganoid fishes may have the edge over teleosts, over and beyond the fact that they are large and mostly live in fresh water, but perhaps aquarists take especially good care of these hard-to-get and eminently displayable creatures. Various diseases and pathological conditions common in aquarium fishes are listed.

S. D. GERKING—"Physiological changes accompanying ageing in fishes"—treats the effect of ageing on nutrition and reproduction. His favoured index of nutrition and growth is nitrogen content, and he finds that the efficiency of protein utilization for growth decreases with increasing size—starting close to 40% in the four species studied and falling as low as 5% in one large sunfish. Data to distinguish possible separate effects of age and size are not available. GERKING points out that this decrease is associated with a continuous decrease, with age, in relative rate of growth in weight.

There are considerable data available concerning change in number of eggs produced, with increasing size and age. Increases in fecundity that are propor-

tional to weight, and some that are more than proportional to weight, have both been authenticated. The oldest specimens of haddock, salmon, etc., apparently produce fewer eggs, even at a given weight, than do somewhat younger ones, but this was not evident in plaice or long rough dab. Actual sterility in middle and old age—so characteristic of mammals—has been observed consistently only in *Gambusia* and in *Heterandria.*

In some fishes it has been found that the within-age regression of log fecundity on log size (weight or length) is less than the overall regression, so that at a given size older fish tend to have more eggs. For Pacific herring GERKING depends on and may rather overvalue the work of KATZ and ERICSON; these authors had few specimens and made no attempt to test the significance of the irregular exponents they computed, at least one of which seems poorly supported by their graphically-presented data. NAGASAKI's (1958) more recent comprehensive study confirms the above effect for the southern British Columbia herring populations but, interestingly enough, shows that it is weak or absent in northern British Columbia. Scottish haddock show the effect rather consistently (RAITT's data) though again tests of significance are not mentioned. In the long rough dab and plaice it has not been demonstrated within single populations, though differences between populations are possible.

Finally, GERKING points out that for four species (Atlantic herring, haddock, long rough dab, and plaice) ovary weight increases more rapidly than number of mature eggs, but it remains unresolved whether the eggs increase in size with size of the fish or whether connective tissue increases in the ovary, or both.

R. J. H. BEVERTON and S. J. HOLT—"A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics"— have the longest paper of these three. Their main contribution is an 8-page table of estimates of growth and natural mortality based on an extensive search of the literature on fishes of all types. The data quoted are the best available, and although uneven in quality, the authors have made an effort to exclude the altogether useless. I was puzzled, however, by the very large natural mortality rates attributed to Columbia River chum salmon: the paper by MARR given as a reference says nothing about natural mortality, and there is no obvious way to estimate it from his data. Growth is presented in terms of the Brody-Bertalanffy parameters L_∞ (estimated average maximum length) and K (rate at which L_∞ is approached), computed for the final stanza of the fish's growth (usually, but not always, from age I onward). Instantaneous rate of natural mortality (M), mean length at maturity (L_m), and maximum observed age in samples (T_{max}), are listed, also the ratio L_m/L_∞. It would perhaps have been useful to specify the kind of length used by each author (standard length, fork length, etc.); as it is, there is about 15% uncertainty in comparing L_∞ between different entries.

An attempt is made to find relationships among the above parameters. The principal possibilities examined are the comparison of T_{max} with L_∞, and of M with K. Some of the graphs obtained look interesting, but it is disappointing that the interpretations suggested usually state well-known facts rather than something previously obscure. For example, from the plots of T_{max} against L_∞ it appears that "the larger members of the herring family ... live to a greater age than do fish ... of comparable size" among the cod, flatfishes, and salmonoids. From the comparison of M and K the main conclusion seems to be

that "the clearly established exceptions to the general positive correlation between longevity and size ... are those species which have a much higher value of K than would be expected from their L_∞". The exceptional groups in question comprise the tunas and the anadromous salmons, which increase in length rapidly at first, then level off abruptly—that is, they grow like herrings instead of like sturgeons or halibut. Incidentally, some readers might have profited by a warning that K, which is called "growth rate" on page 160, is not really a growth-rate in any ordinary sense: of two fishes of the same size and both at least a year into their final stanza of growth, the one with the larger K is growing more *slowly*.

Various comparisons of these parameters are made with other bits of data; these are very definitely tentative, to the extent that it is usually not easy to form an opinion of the reliability or known range of applicability of each. Among those that I tried to track down, there is the statement on page 167 that "with an increase in water temperature K increases roughly proportionally with the logarithm of temperature"; supporting reference is made to experience with only one species, the cod. On page 169 we read: "it would be expected that this [the rate of nitrogen excretion] is also closely related to metabolic rate and to activity, as EDMONDS (1957) has shown in a comparative study of some invertebrate groups". The relationships mentioned may well exist, but it is a considerable overstatement to say that they have been demonstrated by EDMONDS. The latter's nitrogen-excretion experiments were limited to a single species of sipunculid; he compares his results with published work on 6 invertebrates of 3 other phyla, but there is no attempt at an activity rating for them, there are no metabolic studies whatever, and so fundamental a factor as temperature is not considered. Examples of statements which rouse the curiosity, but are unsupported by any data or reference, are (page 166) that "the male natural mortality is greater than the female" among chum salmon, and (page 165) that "trend of mortality with age is abruptly discontinuous" in *Oncorhynchus*, which genus is apparently considered to differ from *Salmo salar* in this respect. We remain uncertain whether the discontinuity in question is the well-known 100% mortality following maturity of sea-run *Oncorhynchus*, or something less familiar.

The short section dealing with metabolism could have been made considerably more informative if WINBERG's (1956) review of fish metabolic rates had been available to the authors. The values of metabolism they quote are a rather small part of what are available; no adjustments to a standard temperature are made to facilitate comparisons with K, M, etc.; and adjustments for weight (w) are made proportional to $w^{\frac{3}{4}}$, in accordance with the now-discredited surface law, instead of to empirically-determined factors (whose average value is about $w^{0.81}$). The short comparison below is based on some of WINBERG's graphs and summary relationships for "routine" metabolism, that is, the oxygen consumption of quiet fish under usual experimental conditions. The K-values are those given by BEVERTON and HOLT, with the addition of values from eye-fitted Walford lines based on data for carp from BALON's (1957) Table 4, for tench from WEATHERLEY's (1959) Table 3, and for pike from MILLER & KENNEDY's (1948) Table 3, and FROST & KIPLING's (1959) Table 6; though estimation of K-values was made difficult by poor agreement with the Brody relationship, especially among tench.

Species or group	Range of K-values	Average routine metabolism at 20°C, as ml of O_2 respired per fish per hour		
		1-g fish	100-g fish	1-kg fish
Anguilla anguilla	0·02	–	9	71
Acipenser spp.	0·04–0·06	0·39	16	105
Esox lucius	0·05–0·45	–	12	77
Perca fluviatilis	0·13–0·20	–	15	–
Tinca tinca	0·15–0·35	0·23	9	54
Cyprinus carpio	0·21–0·42	0·34	17	122
Carassius auratus	"about 0·3"	0·17	7	–
Salmonidae (excluding arctic char)	0·27–0·75	0·50	16	95
Cyprinodontidae	0·8–1·2	0·19	–	–

In the above table, there is obviously little indication of the predicted direct relationship between K and metabolic rate. The question arises, would some more straightforward index of growth, such as weight at a given age, provide any better correlation with routine metabolism? The difficulty of deciding on a representative age-weight table for each species would of course be very considerable, though probably no greater than that of obtaining representative values for K. In the series above, the slow growth of the tiny cyprinodonts is associated with rather low metabolism; while of the three cyprinids, the slow-growing tench and goldfish have a metabolic rate about half that of the much faster-growing carp. However, the most striking characteristic of known average levels of routine metabolism in fish is that, under normal conditions, they are all remarkably similar at any given temperature and weight. Even such differences as do occur may be partly artificial. For example, WINBERG points out that although the difference in routine metabolism between carp and goldfish is one of the largest yet observed among fishes of temperate latitudes, and is completely authenticated technically, nevertheless it *might* merely reflect a greater excitability on the part of carp (especially the larger specimens) which would prevent their metabolism from sinking as close to the "basal" level as the goldfish do, when in a respirometer. Obviously there are numerous avenues yet to be explored, as data become available: for example, instead of "routine" metabolism, comparisons of growth and mortality parameters might be made with basal metabolism, active metabolism at a standard temperature, maximum active metabolism, or "scope for activity" (FRY, 1957).

The final section of BEVERTON and HOLT's paper links up with the subjects considered by NIGRELLI and GERKING. Attention is called to the relation between maturity and death in various species. Particularly interesting are SVÄRDSON's experiments with guppies, in which earliest maturity and shortest life occurred with maximum feeding, while largest size resulted from a moderate rate of feeding. The authors plot L_m, L_∞ against T_{max} for different species, and obtain "just a hint" that short-lived species tend to mature relatively late.

A popular caricature of a biologist is the individual who, having completed an exhaustive and exhausting monograph, describes it as: "An introduction to a preliminary analysis ..." of something or other. This *is* a caricature, but one sufficiently lifelike that it is congenial to come across papers which actually are "progress reports from which tentative conclusions can be drawn", and to find authors so unashamed of this that none considered it necessary to disclaim completeness in his title. We may hope that Messrs. BEVERTON, GERKING,

HOLT, and NIGRELLI will continue to collect information concerning the points they have raised, and that their conclusions will become more numerous and less tentative as time goes on. Meantime, we appreciate being taken into their confidence at an intermediate stage in their studies.

W. E. Ricker

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Announcement

INTERNATIONAL COUNCIL FOR THE EXPLORATION OF THE SEA

Symposium on Zooplankton Production

Following the success of the symposium on primary plankton production held in Bergen in 1957 it is proposed to hold a symposium in Copenhagen in 1961 entitled "Zooplankton Production". It will be held towards the end of the annual session of the International Council for the Exploration of the Sea and will occupy three days: 8., 9., and 10. October 1961.

The symposium will be planned to include:—

A day of 2 sessions on methods of estimating zooplankton, methods used at sea and in the laboratory, methods of assessment of standing crop and production.

One session ($\frac{1}{2}$ day) on the food of zooplankton, the trophic relationships of the organisms, and regeneration of nutrients.

One session ($\frac{1}{2}$ day) on behaviour, including vertical migration, distribution, speed of movement, and zooplankton as a possible source of sonic scattering layers.

One day of 2 sessions left open for extra papers and discussion of recommendations.

This is a very full programme and to keep within the schedule, and yet allow time for the very valuable discussions, the papers at the first four sessions will be by invited speakers only. Papers for consideration for the fifth session will be welcomed, at this stage by title only with a paragraph of explanation if this is not clear in the title. *The sub-committee reserves the right to recommend any paper for presentation to the normal session of the Plankton Committee instead of at the symposium* or because of shortage of time to reject it altogether. Papers for submission to the symposium should not therefore be prepared in detail until approved by the sub-committee.

The success of such a symposium depends as much, if not more, on the discussions as on the papers. It is hoped that a very full complement of experts will attend and take part in the discussions and so ensure a successful outcome. This preliminary notice is therefore made in the hope that as many workers as possible will note the date and make a real effort to attend. So doing will provide an excellent opportunity to meet other workers from all over the world as well as to benefit from the symposium.

In order that contributions can be duplicated and circulated to the participants in advance of the symposium, they will need to be in the hands of the Secretariat by 31. May 1961. Those who wish to contribute a paper to the open sessions should therefore let the convenor know *as soon as possible*, and not later than 1. April. Experts who cannot themselves attend, but would like to submit a paper for circulation only, should send details to the convenor and not later than 1. April. No papers should be submitted in full until accepted by the committee.

If those who intend to make an effort to be present would notify the Convenor as soon as possible it would be a great help, but such an intimation is not to be considered as definite or binding. Further details will be sent later to all who have replied and to any others who ask for them.

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